

**THE EVOLUTION, TAXONOMY AND
STRATIGRAPHICAL SIGNIFICANCE OF
SELECTED CARADOC TRINUCLEID
TRILOBITE
LINEAGES**

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(MSc Thesis)

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Abstract

A new more workable classification of Caradoc cryptolithine trinucleid trilobites is proposed. The classification uses the position of the E2 arc pits in relation to the distinct radial alignment of pits within arcs I_n to E_1 . Most Harnagian species hitherto classified into three genera and five species, namely *Salterolithus caractaci caractaci*, *Salterolithus caractaci paucus*, *Salterolithus praecursor*, *Smeathenia smeathenensis* and *Broeggerolithus harnagensis*, show a pronounced lack of E2 pit alignment with inner arcs. These are now grouped in two species of one genus, *Salterolithus caractaci* and *Salterolithus harnagensis*. The early species show environment sensitive morphotypes in large populations of great diversity. All younger species show distinct radial alignment of E2 pits with the inner arcs. Whilst all these younger species remain within the genus *Broeggerolithus* some have been reclassified to sub species or synonymised as a more population and not typological approach to classification has been adopted. The species *Broeggerolithus broeggeri*, *B. ulrichi*, *B. soudleyensis*, and *B. globiceps* are now subspecies of *Broeggerolithus broeggeri*. *Broeggerolithus longiceps*, *B. melmerbiensis*, *B. aff. discors* are synonymised with *B. nicholsoni*. The type species for *Salterolithus* and *Broeggerolithus* remain unchanged.

Acknowledgements

I would like to thank my two supervisors Alan Owen and Keith Ingham for their guidance and unending patience. Richard Fortey, Claire Mellish, Mike Dorling, Mathew Parkes, Mike Duke and Adrian Rushton for access to the collections in their care. Adrian Rushton for his words of encouragement. My friends and colleagues at Paisley University including Andy Hursthouse for the use of his colour printer. Finally to Simon and my son Calum.

Mum and Dad this is for you.

Declaration

The material presented in this thesis summarises the results of one year of research carried out in the Department of Geology and Applied Geology of Glasgow University under the supervision of Drs A. W. Owen and J. K. Ingham. This study is based on my own independent research and any previously published or unpublished results of other researchers used in this thesis have been given full acknowledgement in the text.

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1 Introduction

The trilobites involved in this study belong to the Subfamily Cryptolithinae of the Family Trinucleidae. They have no eyes. They do however, have a conspicuous bilamellar fringe around the cephalon that contains numerous pits which probably had a sensory function (Chatterton, 1980; Shaw, 1991). The recognition of many trinucleid subfamilies, genera and species is based on pit patterns produced on the fringes. The trilobites of this study are found mainly in Anglo-Welsh deposits of Caradoc age. The Anglo-Welsh cryptolithines appear abruptly in the lower Caradoc (basal Harnagian Substage) with no known local precursors and the origin of these cryptolithine stocks has proved problematical (see Hughes *et al.* 1975, fig 120). The only earlier Ordovician forms that could provide a possible ancestor for the Anglo-Welsh forms and the North American stocks (independently) belong to the genus *Yinpanolithus* Lu, 1974 from China (see Chapter 8). This has a cephalic structure similar to cryptolithine but with only a partially organised fringe and a submarginal girder frontally.

The North American and Czech Republic cryptolithine stocks contain a fixed number of E arcs and a variable number of I arcs. The Anglo-Welsh stocks however, are recognised on the number of E arcs, the number of pits in those arcs and their relationship with the pits in the two I arcs. It has proved increasingly difficult to assign many of these trinucleid trilobites to a named species with any certainty because of the over divisive, largely typological, taxonomy of some previous authors. Too much emphasis has been placed on differentiating morphologically close forms which in many instances occur together in the same beds. Confusion has also been raised by authors ignoring or being unaware of other workers' taxa and erecting their own species names. Thus, for example, Dean's (1960) *Salterolithus praecursor* is remarkably similar to Cave's (1957) *S. caractaci paucus* which Dean did not mention, even though he does refer to Cave's paper. Some specimens of these two "species" are remarkably similar to the previously defined contemporaneous species

Broeggerolithus harnagensis (Bancroft, 1929). Clearly a more population-based approach to the classification of these trilobites is needed that takes into account their occurrences together and their demonstrably overlapping morphologies.

With detailed morphological and statistical analysis, concentrating on fringe features, this study will review critically the taxonomic status of the genera *Salterolithus* Bancroft, 1929, *Broeggerolithus* Lamont, 1935 and *Smeathenia* Dean, 1960 and the species therein. Every effort to include all the relevant taxonomic literature has been taken although the numerous citations of species in formal lists have not been explored. The entire range of these trilobites covers less than about ten million years. They form an interesting case study for the evolution of large, morphologically very variable, interbreeding population to environmentally constrained morphotypes and species. The clarification of the taxonomy will enhance the stratigraphical usefulness of the group.

2 Techniques

2.1 *Material*

All of the samples used for this study were from museum collections, prefixed as follows: the Hunterian Museum, University of Glasgow (HM), the Natural History Museum, London (BM), the British Geological Survey collections, Nottingham (BGS), the Sedgwick Museum, University of Cambridge (SM), the Trinity College Collection, Dublin (TCD) and from the private collection of Nicola Goodwin (NG).

The specimens were studied using a binocular microscope, with magnifications of up to 67.5 x. Fringe pit counts were recorded only where full half-fringe counts were possible (see appendix lodged with the Hunterian museum, for full listings), in the cases where complete cephalae were present both sides were counted. For statistical use alternate fringe halves were used in cases of specimens with complete fringes.

If matrix needed to be removed from the specimen for counting and/or photography then the preparation was carried out using mounted needles and a small engraving drill.

Casts of specimens were produced, if necessary, by using latex rubber liquid dyed with indian ink.

2.2 *Photographic Methods*

The basic approach used for the photography was that based on Siveter (1990). Specimens were cleaned of all dirt, blackened with photographic opaque and whitened using magnesium oxide. Magnification of specimens up to x6 onto negatives was achieved by using a Nikon FM2 camera body with a variety of lenses (24 mm or 55mm), reversing and extension rings, and Ilford Pan F film. The system was set up on a Leitz "Aristophot" photographic stand. Specimens were mounted on a laboratory jack for ease of movement into the focal plane. Standard illumination (low-level from the north-west) of the specimens was achieved using a quartz fibre-optic lamp with back lighting from an angle-poise lamp.

2.3 Statistical Analysis

Historically, trinucleid species have been defined typologically and this approach has proved difficult to use as species show ranges of variation. For example, Dean (1960) highlighted the problem of *Broeggerolithus broeggeri*. For a specimen to be assigned to the species one particular feature it must possess is extra fringe pits mesially. This has meant that specimens from the same population showing identical features, except for extra mesial pits have been relegated to *B. cf. broeggeri*. It has therefore become increasingly common to define and analyse trinucleid species using population statistics based on half-fringe pit characteristics (see Ingham, 1970; Owen and Ingham, 1988). The trinucleid fringe is particularly amenable to such a statistical approach as poorly preserved and incomplete specimens can still be used and therefore identified. This also gives greater numbers of specimens for the study samples and therefore enhanced statistical reliability. This statistical approach depends on the assumption that the trinucleid fringe is symmetrical about the mid-line or that any such differences are not significant in the population sample. Hughes (1970) showed that this is the case in *Trinucleus fimbriatus* Murchison and Section 3.1.1. presents data justifying the approach used in this present study.

Data manipulation and mean, bar and scatter charts based on the various pit counts (see Section 3.1) were produced using the computer package EXCEL 4 run on an IBM compatible and Apple Macintosh computers, this also allowed chi-squared (χ^2) tests to be calculated. Chi-squared tests are used for testing the goodness of fit of theoretical and observed distributions, enabling the comparison of data from one sample with a null hypothesis or between samples themselves. Since the chi-squared test considers the overall shape of the distribution, and not simply the mean and standard deviation, it provides a much more detailed approach than the t or F tests. However, when dealing with very small samples, the chi-squared test may become less accurate though the conclusions can remain valid (see Moroney, 1970).

3 Morphology

Hughes *et al.* (1975) summarised, and partly established, the modern morphological and taxonomic framework for the Trinucleidae. The Family Trinucleidae (Hawle and Corda, 1847) ranges throughout the Ordovician and is known from all the present major continental areas except southern Africa and Antarctica. This family contains trilobites that possess a bilamellar pitted fringe, a marginal suture that is dorsal at the genal angles, genal spines on the lower lamella, a thorax composed of six segments and a triangular pygidium. The trinucleids described herein belong in the Cryptolithinae Angelin, 1854, one of five subfamilies of the Trinucleidae. The Cryptolithinae contains genera whose E, I and F pits are well developed, but unlike the Marrolithinae, I_n is not cut-off posteriorly by the adjacent I arc. The species studied here have previously been ascribed to: *Broeggerolithus* Lamont, 1935 which comprises species with I_n , I_1 , E_1 , and E_2 all essentially complete; *Salterolithus* Bancroft, 1929 which contains species like those of *Broeggerolithus* but with a broader fringe with three E arcs. The pits within the E_3 arc are commonly irregularly positioned and closely packed, in some cases leading to the development of E_4 pits. Finally, *Smeathenia* Dean, 1960 similar to *Broeggerolithus* but with a broader fringe with up to 5 E arcs present, E_3 to E_5 exhibiting varying degrees of irregularity. These three genera are superficially very similar and it is only on detailed analysis of the fringes that consistent differences are seen. This thesis addresses the issue of whether these differences are substantial enough to warrant the retention of these separate genera.

3.1 Cephalic morphology

The cephalon of the species studied here has a semi-circular to angular outline. The glabella is generally clavate and has very weak glabellar furrows. The occipital ring is well developed and well preserved specimens show a posteriorly pointing occipital spine. The glabella is separated from the moderately swollen genal lobes by shallow, straight axial furrows each bearing a deep fossula anteriorly.

Ventrally these fossulae appear as apodemes which may have been sites of muscle attachment or acted as pivots for the hypostoma as in some other trilobites (Hughes *et al.*, 1975). No hypostomes have been recorded from any of the species used in this study and they may have been non- or poorly mineralised structures.

The marginal suture of the bilamellar fringe becomes dorsal posteriorly to include the genal spines in the lower lamella. These paired genal spines are generally three times the sagittal length of the cephalon (excluding occipital spine) and extend well past the pygidium. Their function may have been for stability whilst feeding or to facilitate enrolment. The spines would also have had a protective function, especially when the animal was enrolled.

The lower and upper lamellae are structurally quite distinct, though the narrow funnel-shaped pits pierce both fringe surfaces, so allowing identification from either lamella. Chatterton (1980) reviewed various hypotheses explaining the function of these pits. Two of the more plausible hypothesis are a sensory array for detecting changes in current direction and a gas exchange device. The former could have been useful in helping the trilobite remain stable, as the overall design of the trinucleid is unstable in cross currents. The latter may have been used to supplement their respiration whilst foraging for food in more anoxic environments. These pits are arranged generally in concentric arcs and radial rows. The notation applied to the fringe pits is summarised on Fig. 3.1 and follows that advocated by Hughes *et al.* (1975), based on Bancroft (1929) and subsequent modifications, including that of Ingham (1970). The position of the arcs in relation to the prominent girder on the lower lamella is the basis for the notation. The girder is confluent with the distinctive ridge on the long genal spines. Arcs external to the girder are termed E arcs, and numbered outwards away from the girder. The number of E arcs forms the basis of the present classification of the three genera studied here. All three genera possess two (I) arcs internal to the girder; that nearest to the glabella and genal lobes is " I_n ", the internal arc next to the girder is " I_1 ". Flange pits (F pits) lie between I_n and the posterolateral parts of the genal lobes, and are much smaller than the other pits.

Posterior margin pits (PM pits) lie along the posterior margin of the of the cephalon and include F, I, and E pits. Radial rows are produced when the pits in adjacent arcs are aligned, the first radial row is taken as that row on (R_0) or nearest to the median line (R_1); the two sides of the fringe are numbered separately, sharing only the median row if it is present.

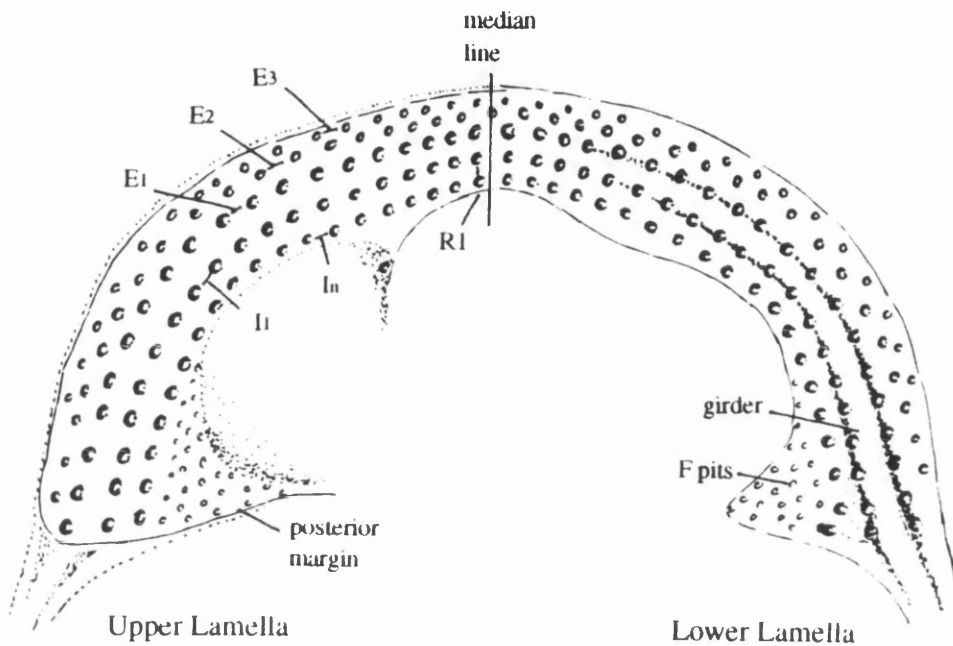


Fig. 3.1 Sketch of upper and lower lamella of Salterolithus caractaci (Murchison, 1839) showing fringe terms.

Another important feature of the external arcs is where they terminate in relation to the most posterior E_1 pit. Thus an E arc extending to the last but one E_1 pit is considered to end at $n-1$, an arc terminating with two E_1 pits posterior to it is said to have a termination of $n-2$ and so on (see Fig. 3.2).

On the upper lamella between each concentric arc of pits a band (list) is present, these lists vary in width and elevation depending on the species and the position on fringe. The lower lamella contains the prominent girder; confluent with the genal spines. Pseudo-girders are present to varying degrees dependent on the species. These features are related to the lists on the upper lamella, between E_1 and I_1 for the girder and lists internal to I_1 for the pseudo-girders.

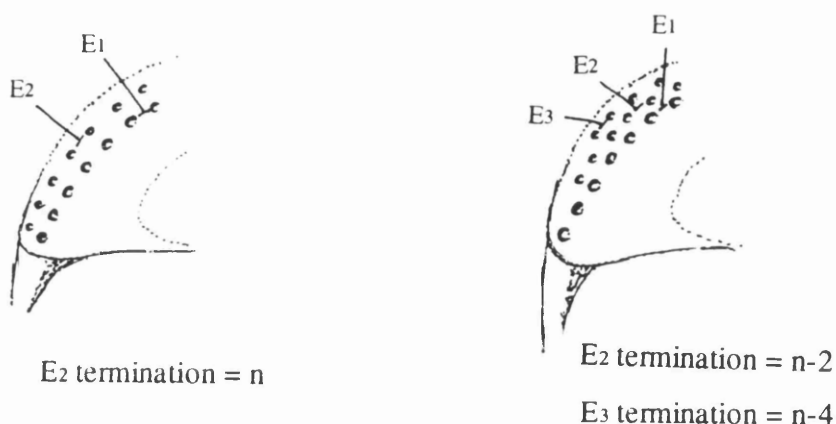


Fig. 3.2 The posterior part of the fringe showing the arc cut-off notation for external arcs. This is determined by how many E_1 pits are between the most posterior pit of the arc and the genal angle.

In some species of *Broeggerolithus* from the early Soudleyan to the Woolstonian, radial ridges, some highly elevated, are present between the pits on the upper lamella. Previous authors have been uncertain as to the importance of these ridges. Bancroft (1949) used the presence of strong radial ridges as one criterion for distinguishing between genera. Whittard (1958) remarked that elevated radial ridges may be an indication of environment and should be used with caution in taxonomy. This study shows a strong link between the environment and the presence or lack of radial ridges and that they can be of taxonomic use, whether it is to distinguish genera, species or morphotypes (see Chapters 5,6 and 7).

Reticulation on the glabella and genal lobes in all three genera is a common feature in the juvenile stages. As individuals progressed into full adulthood this sculpture became restricted to the uppermost areas of the glabella and genal lobes and was then generally lost altogether. Hughes *et al.* (1975) have suggested as possible functions for this cephalic sculpture, camouflage from above or detection of changes in the water flow direction, possibly indicative of predator approach. The latter suggestion reflects the fact that some adults retain reticulation on topographic

highs of their cephalon. In immature individuals the more pronounced development may reflect a greater need for protection or even a different mode of life. Other functions suggested by Hughes *et al.* (1975) were the entrapment of gases for buoyancy or simply strengthening of the exoskeleton.

3.1.1 *Fringe symmetry*

Whittington (1968) noted that owing to the incomplete preservation of the fringe in the bulk of trinucleid material, the vast majority of trinucleid species have been diagnosed on the basis of half or incomplete fringe descriptions, even in species where some complete fringes were known. Indeed, in the three genera being reviewed in this study the type specimens for the species *Broeggerolithus ulrichi* and *B. constrictus* are based on half fringes. The majority of the other species are based on incomplete cephalon or cranidia. It is therefore important to be sure that species are definable without the need for full fringe details. This may only be achieved if the fringe is symmetrical, or any asymmetry must be small enough so as not to have any statistical significance.

The problem of fringe symmetry was addressed by Hughes (1970) using large samples of *Trinucleus fimbriatus* Murchison, 1839. Hughes concluded that: operator errors in selecting half-fringes were negligible, major features of the pit distribution are not dependent on the size of specimen, and statistically there are no significant differences between the left and right half-fringes, although individuals commonly exhibit some asymmetry. Hughes's study is the only work of its kind and as a test of its general applicability, the fringe symmetry in samples of the three genera being studied herein was assessed.

Detailed observations of specimens with one or more characters complete on both sides of the fringe showed that in each sample a range of asymmetry was present with only few of specimens showing any symmetry. No specimen in this study showed symmetry about the mid-line for all concentric arcs of pits. The fringe characters observed were: pit counts for each arc, termination position for outer arcs,

anterior position for the origin of the flange pits, flange pit counts, and the number of pits along the posterior margin. The graphs in Fig 3.3 show the distribution of characters in the species as presently defined. Depending on the species and the character being considered, the degree of asymmetry ranges from a narrow band of up to two pits (e.g. E_1) to a wide range of up to six pits as in I_n and I_1 . Significance tests were not carried out as the data samples are too small for accurate calculations. To prevent biasing the data because of the asymmetry present alternate left and right half-fringes of complete specimens in the data matrix were used in compiling population sample data.

Misidentification of the median line could lead to an apparent asymmetry of one or two pits in a symmetrical individual. For instance a specimen having $2n + 1$ pits (full fringe) in a particular arc would appear symmetrical (with regard to that arc) if the mid-line were taken along the central median row, but asymmetrical if taken along either adjacent ridges or rows (Hughes, 1970). In order to reduce such misidentifications to a minimum at least in specimens with a little more than a half-fringe present, the sagittal line was taken as passing through the mid point between the anterior fossulae, allowing for any tectonic distortions. This median line can lie along a radial row of pits, a radial ridge or in specimens with non-radial alignment of pits mesially the mid line can encompass both ridges and pits in different arcs. Pits which lay along the median line were counted as half a pit. Where the lower lamella was present only, the median line was taken as that which passed through the indentation in the lower lamella into which the tip of the pygidium fitted during enrollment.

The types of asymmetry noted above should not be confused with that of abnormal fringes which may have arisen through repair of an injury, teratology (genetic or embryological malfunction) or pathological conditions (disease or parasitic infestation) (see Owen, 1983, 1985 for more details). However, these types of asymmetries may occasionally go undetected, because of advanced repair of an injury or minor teratological or pathological conditions.

Another important point discussed by Hughes (1970) was that pit distribution and the number of pits per arc are features not dependent on the size of the individual. The fringe assumes the essential adult characteristics very early in the meraspid stage of development (Whittington, 1941 and 1959). The number of pits on the fringe is therefore genetic and is not to do with ontogeny (age). This is an important consideration when dealing with small numbers of specimens of limited size range. Analysis of the largest sample in this study compared specimens larger than 1 cm across the cephalon at its widest point with specimens less than 1 cm across and found there to be very little difference in pit numbers for similar arcs. A slight increase in F pit counts was seen in the larger specimens compared to smaller individuals. The addition of a few pits in the larger specimens may be a reflection of increased size. It is uncertain whether the small specimens were holaspides as no complete specimens were present. A much larger sample size would be needed to see if these results were significant.

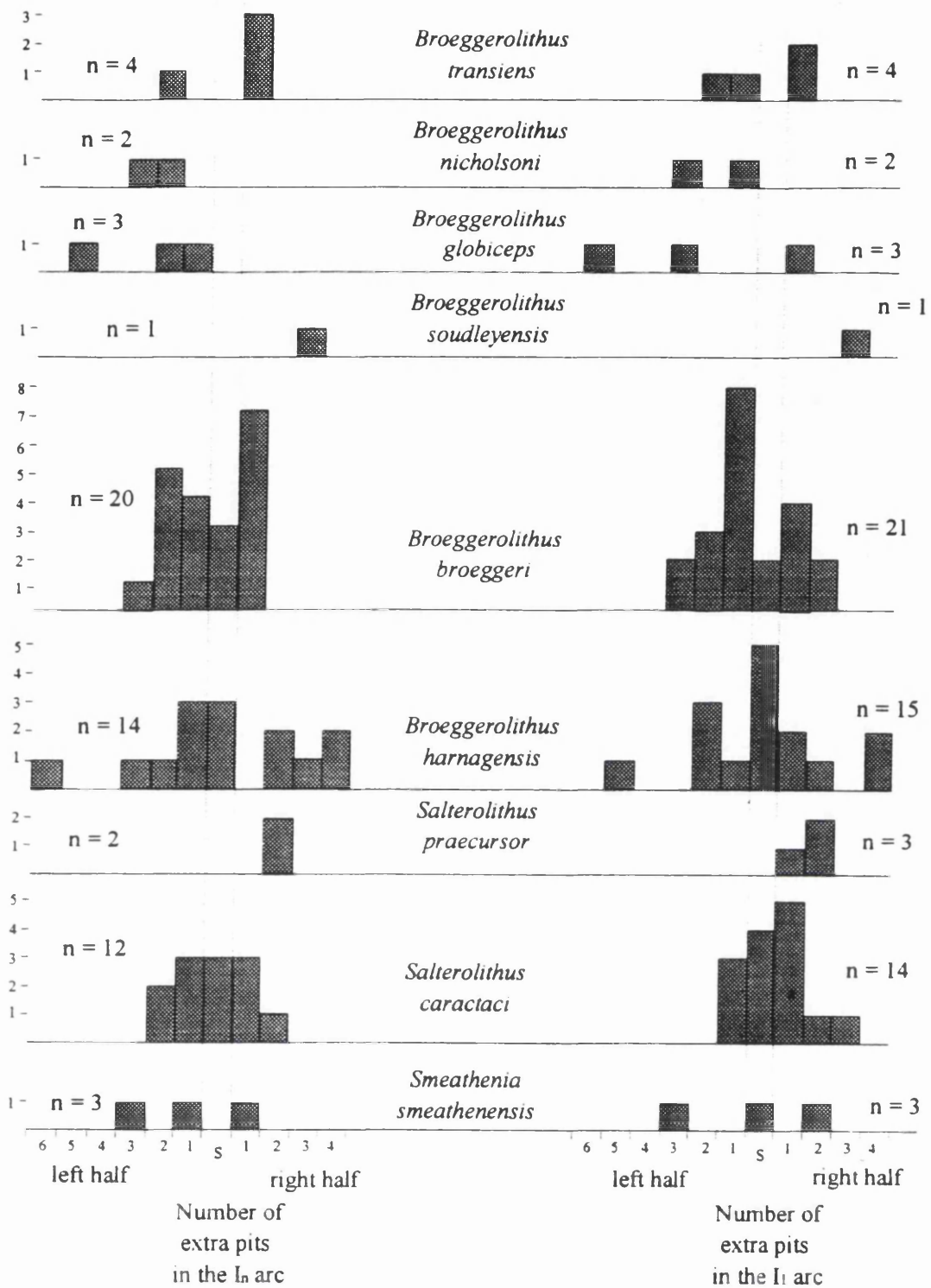


Fig. 3.3 (a) Diagram showing the asymmetry of arcs I_n and I_l of species as hitherto defined. The number of pits in each fringe half is compared and any difference in the count is displayed on the relevant fringe half. If the number of pits is equal on both sides of the fringe then the specimen is symmetrical about that arc and noted in the "s" column.

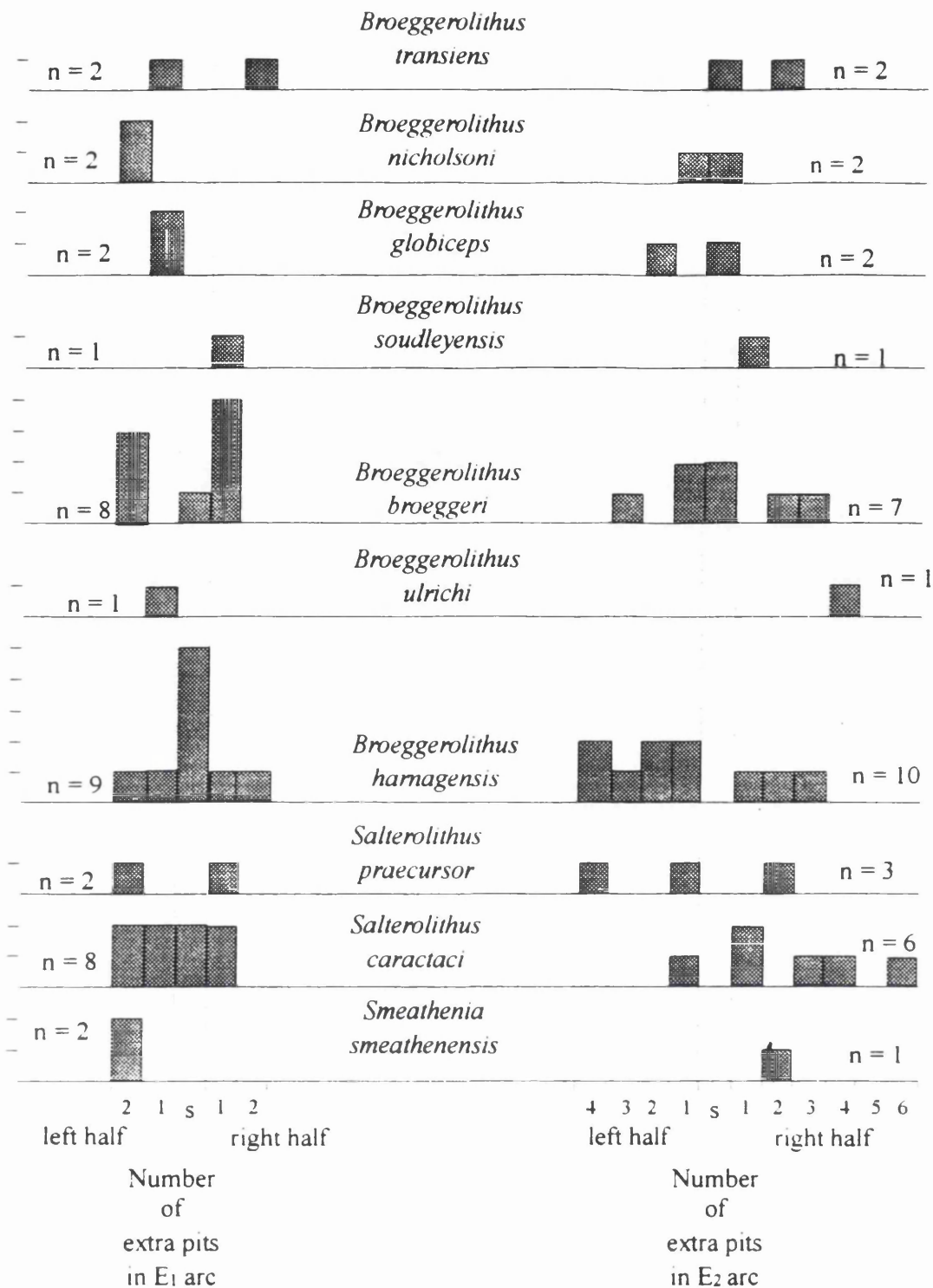


Fig. 3.3 (b)Diagram showing the asymmetry of arcs E1 and E2 of species as hitherto defined. The number of pits in each fringe half is compared and any difference in the count is displayed on the relevant fringe half. If the number of pits is equal on both sides of the fringe then the specimen is symmetrical about that arc and noted in the "s" column.

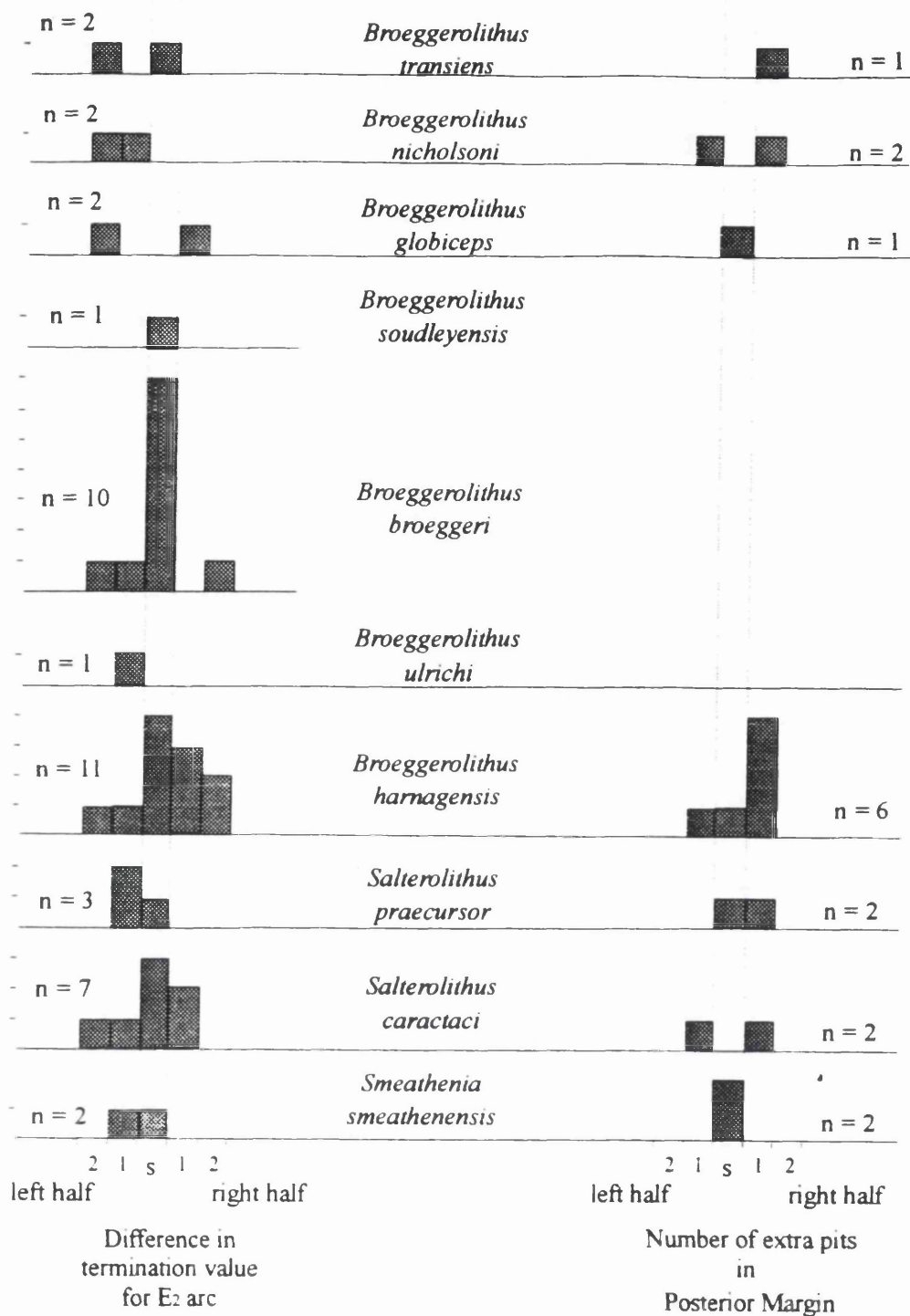


Fig. 3.3 (c) Diagram showing the asymmetry of the position of the most posterior E2 pit (relative to E1 arc pits) and the number of pits along the posterior margin of species as hitherto defined. Any variation between the two halves is displayed on the relevant diagram fringe half. If the specimen is equal on both sides of the fringe then the specimen is symmetrical about that feature and noted in the "s" column.

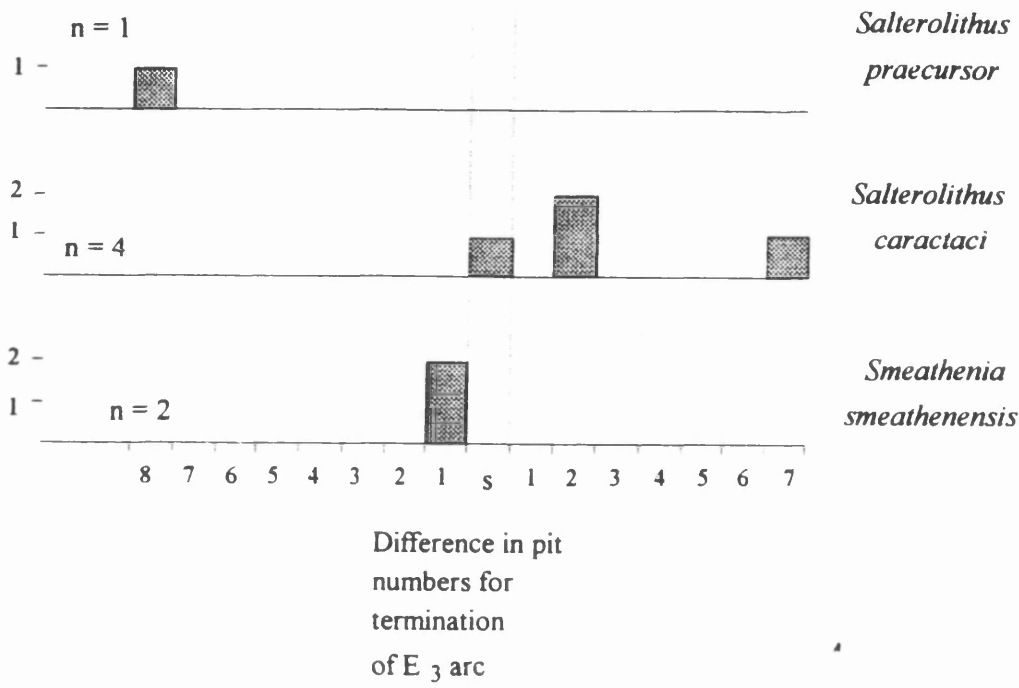


Fig. 3.3 (d) Diagram showing the asymmetry of the position of the most posterior E₃ pit (relative to E₁ arc pits) of species as hitherto defined. Any variation between the two halves is displayed on the relevant diagram fringe half. If the specimen is equal on both sides of the fringe then the specimen is symmetrical about that feature and noted in the "s" column.

3.2 Thoracic and pygidial morphology

In all three genera studied, the thorax and pygidium are very similar, so much so that it is impossible to identify separate species, let alone genera by these tagmata alone. The thorax, like that of all trinucleids, contains six segments in the holaspis stage. The pygidium is sub-triangular, with axial rings and pleural ribs becoming indistinct posteriorly. The number of axial rings and pleural ribs varies within a species and even between the internal mould and external surface moulds of individual specimens. For the species in this study the shape of the pygidia is directly proportional to the size of the individual, regardless of species (see Fig 3.4). The pygidia therefore are of no reliable taxonomic use in these species.

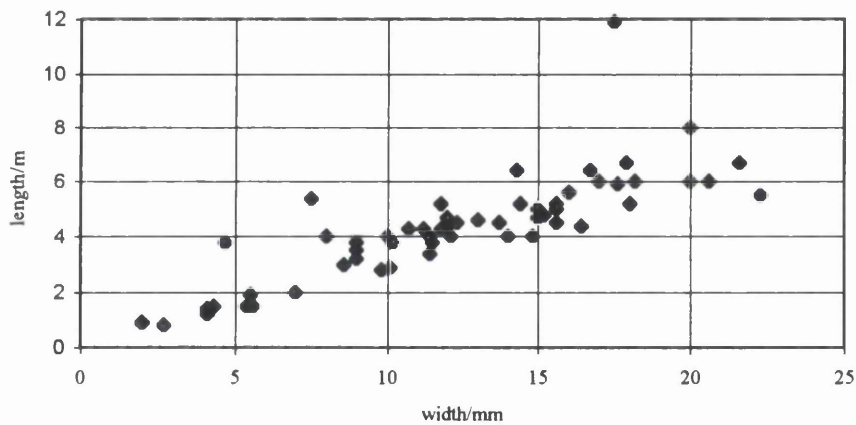


Fig. 3.4. Graph showing the sagittal length against maximum width for all complete or partially complete pygidia found in this study. The linear nature of the data suggests any variation in shape is connected to the size of the individual trilobite.

4 Stratigraphical Framework

The material used in this study has been collected from Wales, the Welsh Borderland (Shropshire), Northern England and South-eastern Ireland (see Fig 4.1) and Scandinavia. The majority of samples are from South Shropshire, the historical type area of the Caradoc Series and its component stages and substages.

Bancroft worked extensively in the Welsh Borderland and erected stages within the Caradoc Series based on trilobite and brachiopod assemblages (1929, 1929a, 1933, 1945). Bancroft's stages have considerable value in correlation within Britain and to some extent further afield. His biozones include those of *Salterolithus caractaci*, *Broeggerolithus harnagensis*, *B. ulrichi*, *B. broeggeri* and *B. soudleyensis*. All of these species being reviewed in this study. Bancroft did not define precisely the boundaries of the Caradoc stages. Dean (1958) reviewed Bancroft's work and later Hurst (1979) documented the upper Caradoc and introduced the term "Woolstonian" for what Bancroft (1933) and subsequent authors called the Upper Longvillian. The latest revision of the Ordovician System in Britain (Fortey *et al.*, 1995) has proposed new stages for the type Caradoc to facilitate easier correlation outside Britain; Bancroft's stages being retained as substages, see Fig. 4.2.

The base of the Caradoc is now defined at the base of the *Nemagraptus gracilis* Biozone - a level that is missing in South Shropshire as the basal Costonian beds, resting unconformably on older strata lie within this biozone (Fortey *et al.*, 1995). The Caradoc history of the British Isles is closely related to the closing of the Iapetus Ocean. The near to off shore deposits were influenced by regional and global marine transgressions and regressions and by localised volcanic activity. The deposits are mainly sandstones, shales, mudstones and siltstones. Local names have been given to lithologically similar, coeval beds in the past by workers (e.g. Dean, 1958) concentrating on local areas in the type area of the Caradoc. For example, in Southern Shropshire the late Soudleyan-Longvillian banded sandstones, which have

been extensively quarried in the past for local building stone, are known as the Horderley, Soudley or Chatwall Sandstones depending on their outcrop area. Similarly, the Harnage Shales and Chatwall Flags are known further south as the Smeathen Wood Beds and Glenburrell Beds respectively (see Fig. 4.3). Correlation charts of the main sample areas in South Shropshire, Wales and North England are shown in Fig. 4.4.



Fig. 4.1. Location map of the main sample areas within Britain and Ireland.

Location 1: southern South Shropshire, 2: northern South Shropshire, 3: Shelve Inlier, 4: Welshpool, 5: Snowdon, 6: Arenig - Bala, 7: north Lake District, 8; Cross Fell Inlier, 9: Kildare Inlier and 10: Slieveroe.

Epoch	Stages	Substages	British graptolite Biozones
CARADOC	Streffordian	Onnian	<i>linearis</i> ? ?
		Actonian	
	Cheneyan	Marshbrookian	<i>clingani</i>
		Woolstonian	
	Burrellian	Longvillian	? ?
		Soudleyan	
		Harnagian	<i>foliaceus</i> [= <i>multidens</i>]
	Aurelucian	Costonian	<i>gracilis</i>
		Velfreyan	

Fig. 4.2. Revised chronostratigraphy of the Caradoc Series with new stages and substages, after Fortey et al.,(1995).

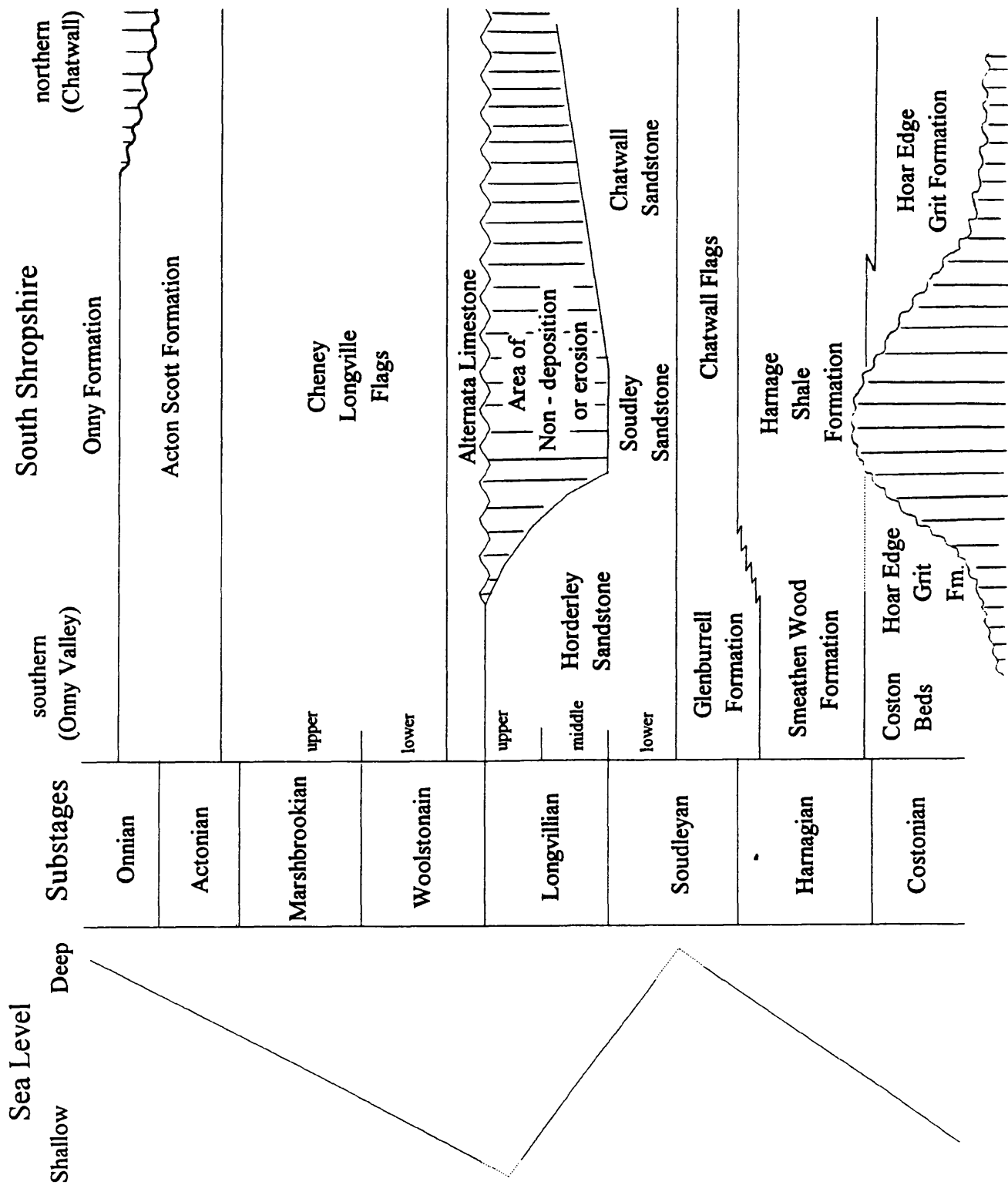


Fig. 4.3. Sketch of South Shropshire lithology showing local names of deposits and the eustatic sea level changes for this area (after Hurst, 1979 and pers. comm. Dr. J. K. Ingham).

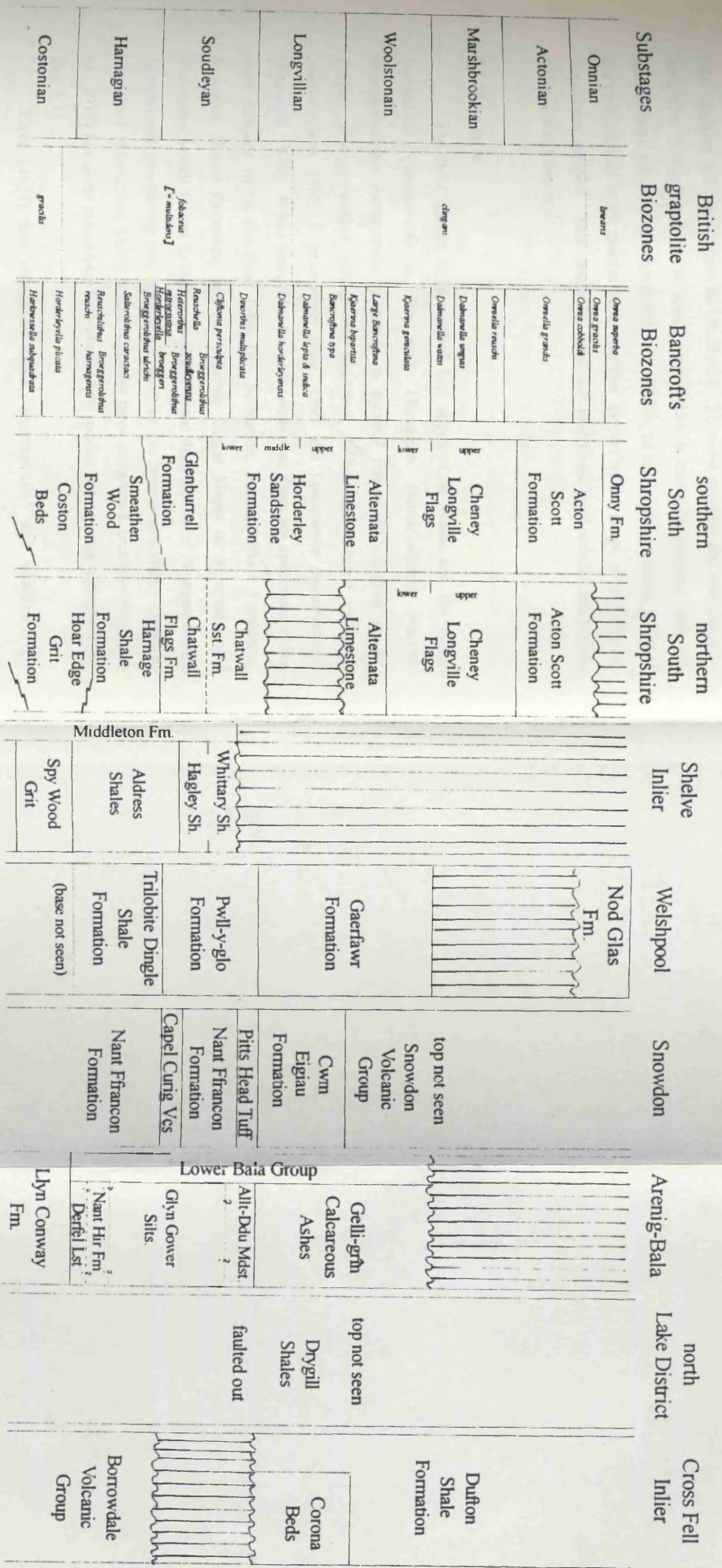


Fig. 4.4 Correlation Charts of the main British sample areas. Refer to Fig. 4.2 for Stages. After: Pratt (1995), Kneller et al (1994), Zalasiewicz (1992), Arthurton (1981), Burgess (1979), Hurst (1979), Williams et al (1972), Craig (1968), Whittington (1966), Dean (1962 and 1960), Cane (1965), Bancroft (1933).

5 Temporal and spatial analysis

In this analysis chapter the existing taxonomic names will be used and only in later chapters will any changes be introduced. To avoid creating any interpretative bias, after noting the genus to which each species is currently assigned, only the species name will be used subsequently. In addition, as will be shown below, some of the typologically based species occur together as part of the range of variation of population samples. This clearly has profound taxonomic implications that will be addressed in Chapter 6.

5.1 Harnagian

The three genera being studied first appeared in Wales and the Welsh Borderland (Shropshire) in the early Harnagian (*Reuscholithus reuschi-Broeggerolithus harnagensis* Biozone), in material historically assigned to the species: *Broeggerolithus harnagensis* (Bancroft, 1929), *Salterolithus caractaci paucus* Cave, 1957, *S. praecursor* Dean, 1960 and *Smeathenia smeathenensis* (Bancroft, 1949). It had been clear for some while that there are specimens within most samples within the Hoar Edge Grit Formation, Harnage Shale Formation, Smeathen Wood Formation and the Trilobite Dingle Shales of Shropshire and Welshpool which do not fit the typologically based descriptions of *Broeggerolithus harnagensis* (containing two complete E arcs) or the later *Salterolithus caractaci caractaci* (Murchison, 1839), which possesses three complete E arcs (see Hughes *et al.*, 1975) but come somewhere between the two species and co-exist with them (see Fig. 5.1).

Cave (1957) first recognised these "intermediates" and established the subspecies *Salterolithus caractaci paucus*, characterised by an E₃ arc present as intercalations in the E₂ arc anterior to the glabella and the number of pits outside of arc E₁ being considerably less than in *Salterolithus caractaci* (from the lower Harnagian Trilobite Dingle Shales, at the north end of Trilobite Dingle, Welshpool). Dean (1960) established *Salterolithus praecursor* (from the lower Harnage Shale Formation in Coundmoor Brook, Shropshire) containing three E arcs which are complete or nearly complete. He gave figures for the sum of pits of both E₂ and E₃,

but he did not mention to what extent these E₃ arcs were present. Indeed the variation in E₃ formation is very large between the holotype of *praecursor* and other specimens which Dean figured to illustrate his species, such as BM. In 52031, a paratype with E₃ extending posterolaterally and BM. In 52041, which contains E₃ as merely a few pits in a zigzag arrangement with the E₂ arc anterolaterally (see Plate 1, Figs. 1 and 2). Dean also neglected to mention Cave's *caractaci paucus*, which is very similar to some *praecursor* specimens (see Fig. 5.1).

The "species" *smeathenensis* is very similar to the contemporaneous *praecursor* except that it contains four or more E arcs (see Fig. 5.1). Its type locality is in the Smeathen Wood Formation, in the south-eastern corner of Smeathen Wood, Shropshire, and it is also found in other locations in northern and southern South Shropshire as a rare member of the populations there.

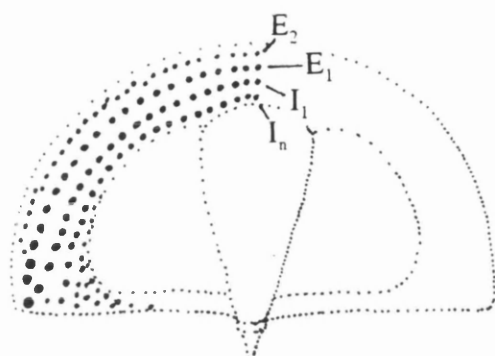
The four "species" which have been described above from the early Harnagian of Wales and Shropshire namely *harnagensis*, *caractaci paucus*, *praecursor*, and *smeathenensis* are commonly found together (e.g. Plate 1, Fig. 3) in varying proportions and only differ in their number of E pits and E arcs. This morphological gradation between "species" suggests that the clearly defined typological classifications used at present may not provide a true representation of these populations and the morphotypes therein. Table 5.1. summarises this complex assemblage of morphotypes found in the early to middle Harnagian. The table also includes the younger *caractaci caractaci* for later reference. It is argued below that because of their overlapping morphological and statistical characteristics, with the exception of the younger *caractaci caractaci*, they must all be part of one large interbreeding species and not discrete species as hitherto believed.

The "species" *caractaci caractaci* (Murchison, 1839) is found in Shropshire, Wales and the Shelve Inlier from the upper Harnagian up into beds of early Soudleyan age and it is the dominant form in the Harnage Shale Formation of northern South Shropshire assigned to the *Salterolithus caractaci* Biozone. Dean (1960) noted that *c. caractaci* is similar to *praecursor* but generally contains higher pit counts for all arcs, an E₄ arc is present in some specimens, the cephalic outline is more angular, the lists on the upper lamella are broader and the overall size is larger

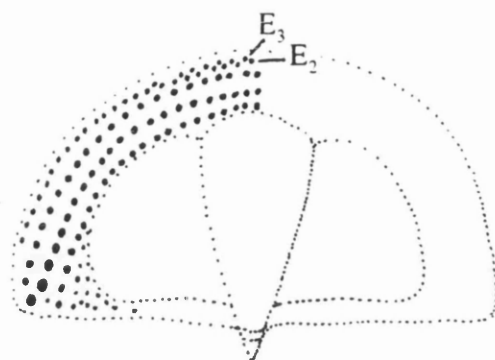
than *praecursor*. The occasional presence of an E₄ arc, along with high pit counts in *c. caractaci* also provides a strong similarity to the earlier *smeathenensis*.

Species as hitherto defined	Number of E arcs	Extent and position of pits in outer most E arc	Number of pits in E ₃ arc (approx.)
<i>harnagensis</i>	2	complete	none
<i>caractaci paucus</i>	3	anterior	<10
<i>praecursor</i>	3	anterior to posterolateral	<20
<i>praecursor</i>	3	complete	> = 20
<i>caractaci caractaci</i>	3 rarely 4	complete	>20
<i>smeathenensis</i>	greater or equal to 4	anterior to posterolateral	>20

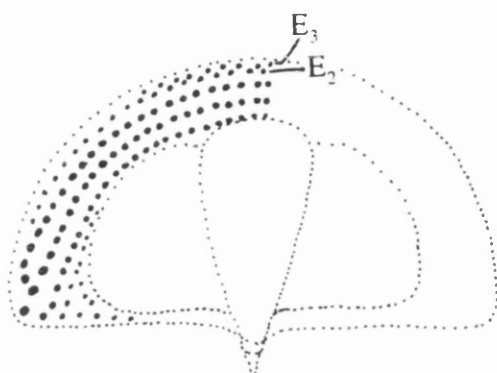
Table 5.1. The morphotypes present in the Harnagian of Wales and Shropshire. All show misalignment of E₂ pits with radial rows of inner arc pits. harnagensis is found in lower beds in both areas, caractaci paucus in lower beds of Wales, praecursor in lower beds of Shropshire, caractaci caractaci in upper beds of both areas and smeathenensis, a rare member, is found in lower beds of both areas.



harnagensis

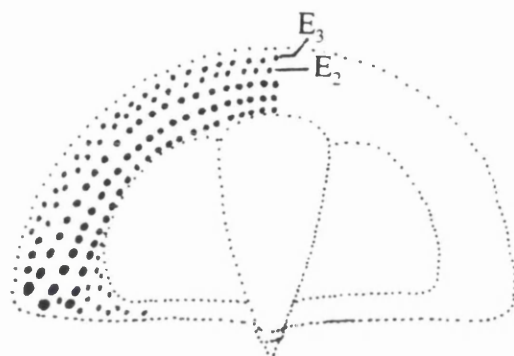


caractaci paucus

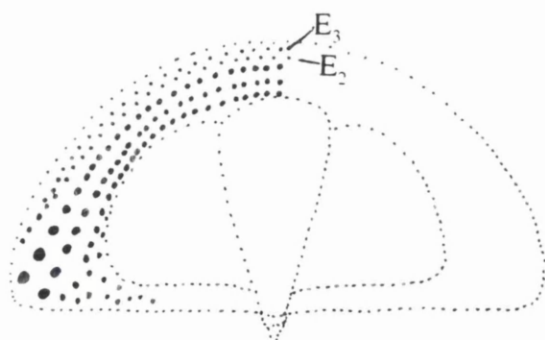


(low E3 pit count)

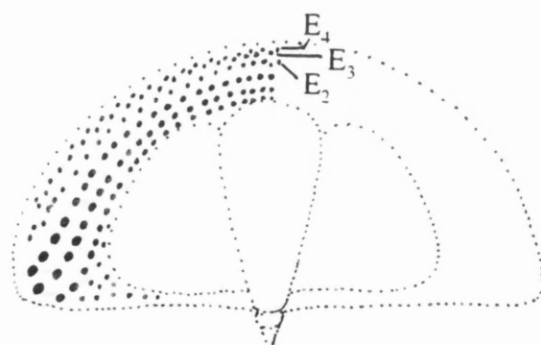
praecursor



(high E3 pit count)



caractaci caractaci



smeathenensis

Fig. 5.1. Sketches of the different morphotypes present in the Harnagian of Wales and South Shropshire. Fringe pit distributions are shown only on one side of the cephalon. Sketches not to scale.

Cave (1957) gave detailed locations for his samples of *caractaci caractaci* and *caractaci paucus* from Trilobite Dingle, Welshpool. Unfortunately, most museum samples, except for Cave's, are not documented well enough to fix their precise location in the section and are therefore, of little use statistically. Cave recognised morphological differences between *c. paucus* and *c. caractaci* and that the *c. paucus* specimens came from locations in the northern part of the dingle, which he quotes as the "top of the succession". Morphologically *c. paucus* is indistinguishable from some *praecursor* specimens from the early Harnagian of Shropshire. On close inspection of the beds in Trilobite Dingle, see Fig. 5.2, the succession goes from grey/green mudstones that are steeply dipping in the south through an area consisting of red-stained mudstones then a gap with no exposure to gently dipping dark mudstones with good exposure at the northern end of the dingle. Iron oxide from the younger Permian deposits could have been leached down into the older Harnagian beds producing the characteristic red-staining. From these observations it is clear that an east-west trending fault up throwing to the north has brought older unstained mudstones bearing specimens of *c. paucus* up to the same level as the younger beds containing the late Harnagian *c. caractaci* (Dr. J. K. Ingham pers comm. 1994). There are numerous east-west trending faults in the surrounding area (Cave and Price, 1978) that are parallel to that postulated in the dingle. Therefore, *c. paucus* is likely to be a lower Harnagian form and not as Cave thought a late Harnagian species. If this is the case *S. c. paucus* and its morphological contemporary *S. praecursor* are synonymous with one another. Cave (1957) synonymized *S. intermedius* (Wade, 1911) with *caractaci caractaci* on lithological and statistical grounds, this view is supported here.

Close similarities between all the "species" from the lower Harnagian are clearly observed when the statistical data for the mean and range variation values for pit numbers per arc are displayed (see Figs. 5.3 and 5.4). Fig. 5.3 displays data from specimens found in material from the early and late Harnagian of northern and

southern South Shropshire. Charts (a) - (f) display means and ranges for species as hitherto defined and charts (g) - (l) show data in histogram form. All these charts show closely related values for arcs I_1 and E_1 and (k) and (l) show step like progression of the data from *harnagensis* to *smeathenensis* when comparing the total number of pits outside arc E_1 . Fig. 5.4 shows the data of Trilobite Dingle Shale Formation specimens, (a) - (f) give mean and range charts and (g) - (q) show the data in histogram form. All graphs show the different species as hitherto defined have closely related values and show a step like progression from *harnagensis* to high pit count *caractaci paucus*. A general trend towards higher pit counts can be seen from lower to upper Trilobite Dingle Formation. These charts also give a general indication of the morphotypes present within the populations from different environments, *harnagensis*, *c. paucus* and *praecursor* appear in greater numbers in the shallow early Harnagian and *c. caractaci* in deeper waters in the late Harnagian. For these morphotypes within each population the majority of their mean pit counts are within a two pit difference and their ranges of pit counts overlap. These differences are not great enough to distinguish the different forms and therefore cannot be used as criteria for classification.

Figs 5.3 and 5.4 show that the ranges of pit counts for I_1 , E_1 and the sum of pits outside arc E_1 for all early Harnagian forms overlap considerably. In northern South Shropshire, where *praecursor* is most common, I_1 and E_1 arc pit count ranges and means for *harnagensis* and *praecursor* are indistinguishable and it is only in the sum of all pits outside E_1 that any difference is seen. This difference can be explained by the addition of an E_3 arc in *praecursor* and explains a similar result seen in Welshpool, where *c. paucus* is found. This gradation from low to high pit counts within the population without any significant breaks would suggest that the specimens were morphotypes of one large interbreeding population rather than discrete species.

The Chart 5.4 (n) shows E_3 pit radius numbers for *praecursor*, *c. paucus*, *smeathenensis* and *c. caractaci* specimens and gives an indication of the wide variation in pit numbers. Fig. 5.4(p) shows that the E_3 arc of the older *praecursor* specimens extend the same distance around the fringe as the E_3 arcs in *c. caractaci*, this feature produces the compact often irregular pit distribution seen in *c. caractaci*

particularly anteriorly, which is generally not present in *praecursor* (see Pl. 1, Figs 1 and 6). The E₃ arc pit radius numbers for *smeathenensis* show a lack of specimens containing between 27 and 29 E₃ pits, see Fig 5.4 (n). The E₃ pit pattern for specimens containing more than 29 pits is more closely packed and often more irregular than an E₃ arc with less than 29 pits. This grouping of specimens into two categories one containing those which have less than 27 E₃ pits and those which have more than 27 pits could assist in morphological discrimination. The "species" *smeathenensis* shows a wide variation of numbers in the E₄ arc (2-36 pits) see chart Fig. 5.4 (q). This shows numerous breaks in the pit range for the E₄ arc and because of the general irregularity of pits in this arc making identification of an E₅ arc difficult in some instances, it is considered here that two morphotypes be chosen, one containing less than 27 E₃ pits and between 2-23 E₄ pits, the other containing more than 27 E₃ pits and between 2-36 E₄ pits with occasional E₅ arc pits present.

Within the early Harnagian population of Welshpool there are rare specimens with high E₃ pit counts. The chi-squared tests show for the high E₃ pit count *c. paucus* forms and *c. caractaci* forms in the Welshpool area there is no significant difference at the 95% confidence level. This would suggest that on statistical grounds specimens similar to *c. caractaci* had appeared in the early Harnagian as rare members of the variable population. If a population based classification is to be used then these early forms which are clearly precursors to *c. caractaci* are only a variety within a variable population and can not be classed as a separate species. Some late Harnagian specimens show low E₃ pit counts similar to earlier *c. paucus/praecursor* forms. These rare forms had survived within the population well into the late Harnagian as a variant of the dominant *c. caractaci* form.

Statistically, a clear link has now been shown (Figs 5.3 and 5.4 and Table 5.1) between the present "genera" and "species" in the Harnagian. To confirm this link morphological trends within those populations need to be studied, particularly the fringe pit patterns. The basic pit distribution patterns of the different morphotypes are displayed in Fig. 5.1. All three "genera" show the same basic pit pattern for the first three arcs (I_n-E₁) and only appear to be different in the pit patterns in arcs outside E₁. The morphotype *harnagensis* shows a general radial pit alignment between I_n and E₁, which persists posterolaterally. Of major importance to the new

classification (see Chapter 8) E_2 is out of pit radial alignment with the inner arcs, having more pits than E_1 (Plate 1, Figs, 3 and 4). A minority show E_2 radially aligned anteriorly but this does not usually persist beyond the level of the axial furrow. Specimens of *c. paucus* and *praecursor* show similar pit arrangements to that of *harnagensis*, with the extra E_3 arc pits aligned with the inner three arcs and E_2 staggered between E_1 and E_3 . Pits in arcs I_n to E_1 tend to be large and usually increase in size posteriorly, whilst pits of E_2 and E_3 arcs are small over the whole fringe (Plate 1, Fig. 5). The species *c. caractaci* shows the same pit patterns as high E_3 pit count *praecursor* with E_3 extending towards the genal angle (Plate 1, Fig. 6). The minority of *c. caractaci* which contain an E_4 arc and all *smeathenensis* forms show this pit arrangement, with the extra E arcs staggering their pit positions with the previous arcs (Plate 1, Fig. 7).

In the past, importance has been placed on the shape of the outline of the cephalon in distinguishing species, for example *praecursor* has a more rounded cephalic outline than *c. caractaci* (Dean 1960; see also Fig. 5.1 herein). The shape of the cephalic outline is the direct result of fringe pit positioning and the size of the pits with pits increasing in size anteriorly to posteriorly producing a wider fringe posteriorly. The majority of *praecursor* forms contain outer arc pits anteriorly to posterolaterally creating a wider fringe anteriorly. This makes the fringe appear more rounded than *c. caractaci* whose outer arc of pits continues posteriorly. It is therefore, more important to understand the relationships of the pit patterns rather than using cephalic outline as a classification aid as this can be easily deformed during sediment compaction. In a minority of individuals of any of the morphotypes all the pits appear to be the same size (Plate 1, Fig. 8), but the significance of this is not clear.

Some individuals show pits which appear in pairs with a thin wall between them, giving the impression of a single pit splitting into two. This most commonly occurs in *c. paucus* and *praecursor* morphotypes (Plate 1, Figs. 9, 10 and 11). These pits are usually in the outermost arc of the fringe, they appear sulcate due to the prominent radial ridges either side of the pits and the lack of any radial band between the two pits. Without the presence of successive moulted fringes of the individual trilobite it is difficult to speculate on the nature of these paired pits.

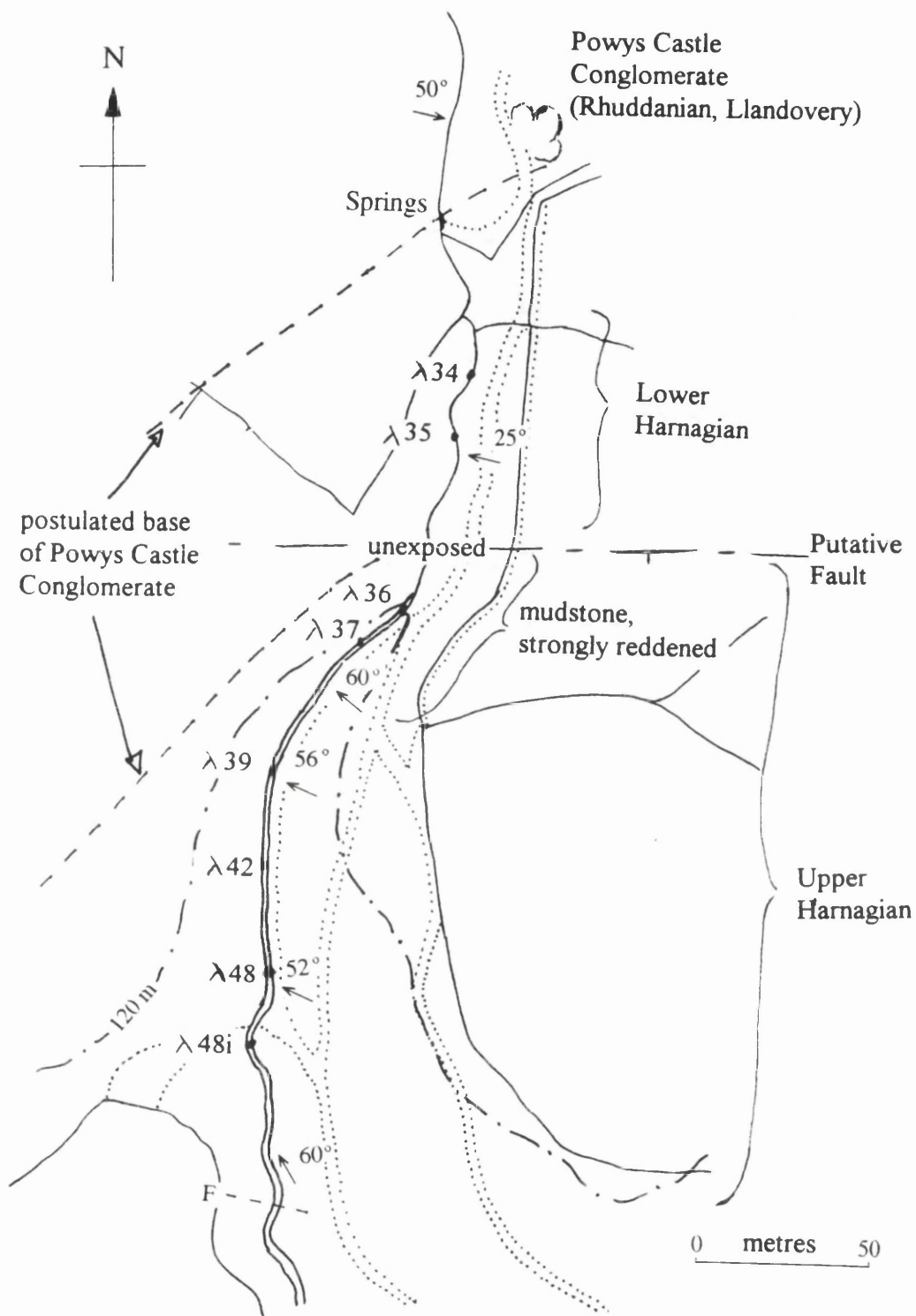


Fig. 5.2. Sketch-map of Trilobite Dingle, Welshpool based on Cave (1957) and J. K. Ingham (pers comm. 1994). Caves original locations are shown.

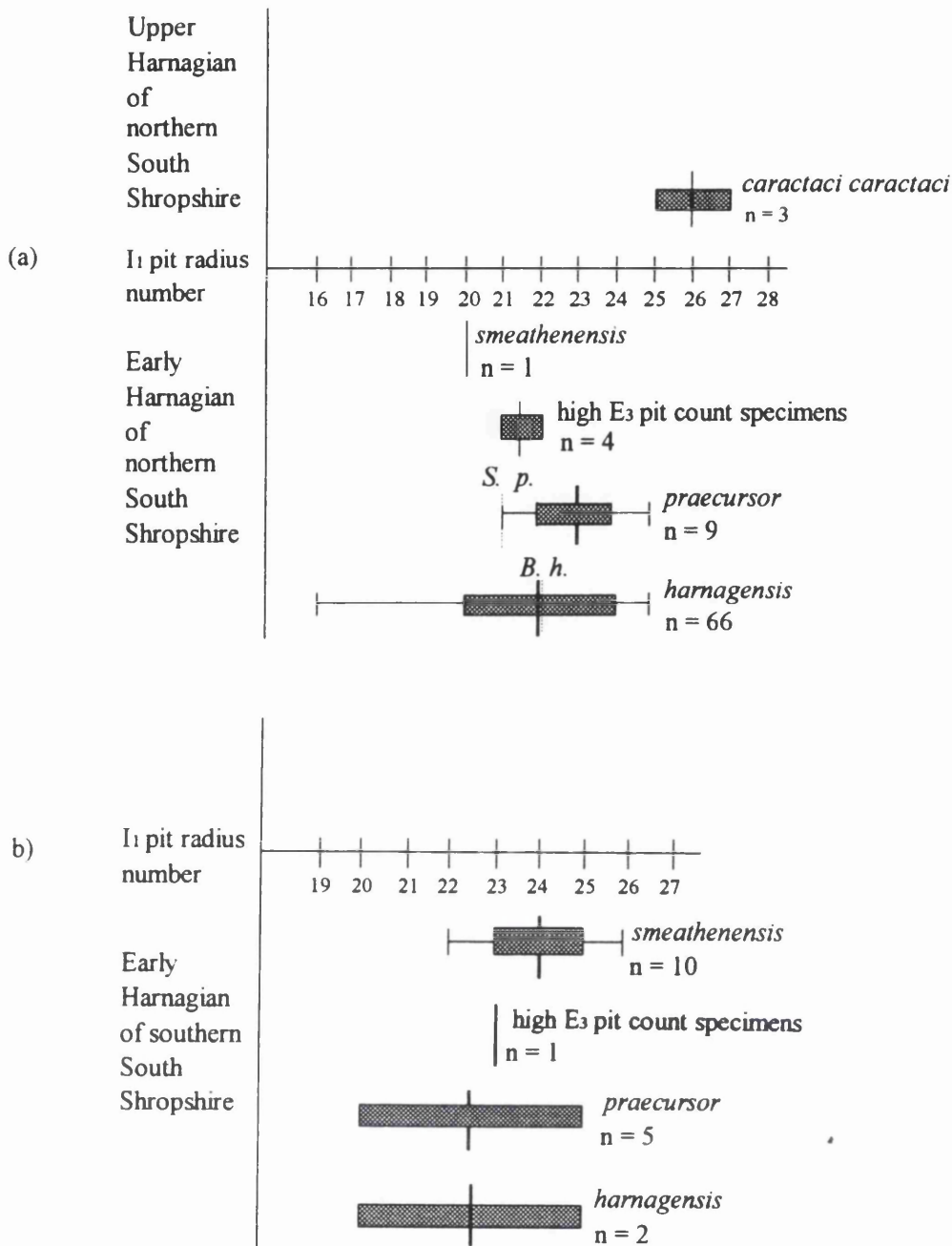


Fig. 5.3 Range and mean charts showing I1 pit radius number for species as hitherto defined from (a) northern South Shropshire and (b) southern South Shropshire. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line.

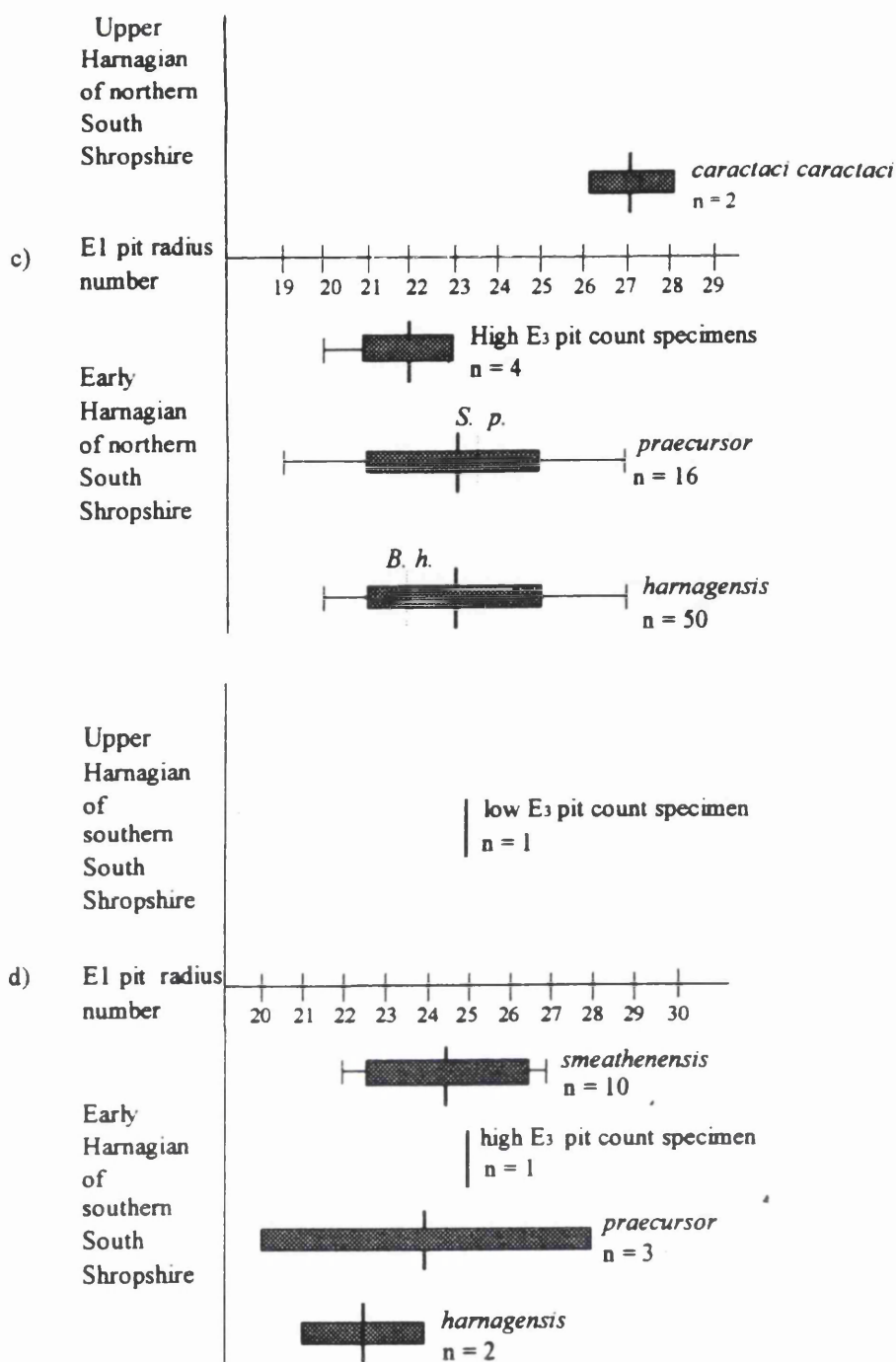


Fig. 5.3 Range and mean charts showing E1 pit radius number for species as hitherto defined from (c) northern South Shropshire and (d) southern South Shropshire. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line.

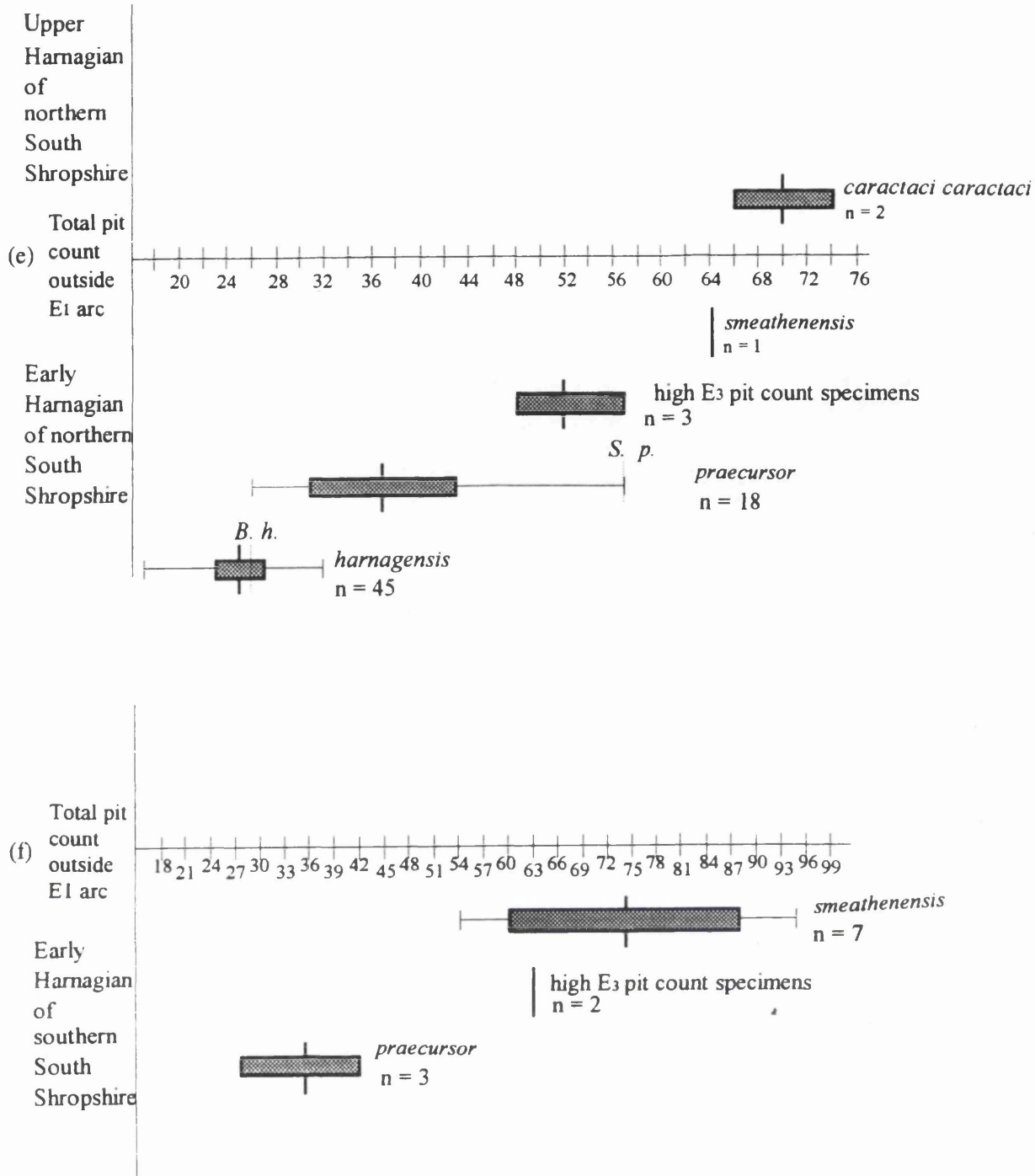
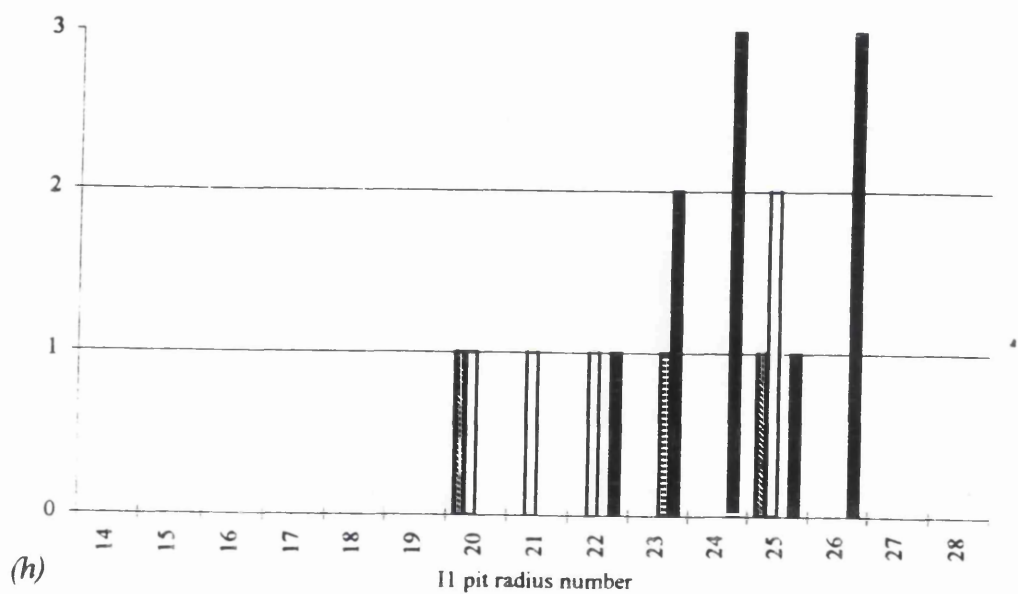
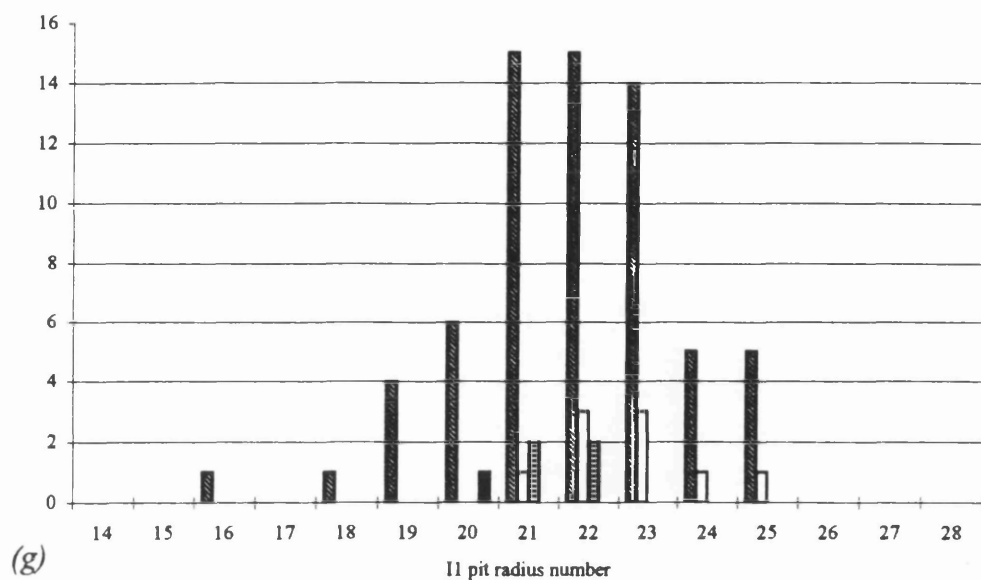
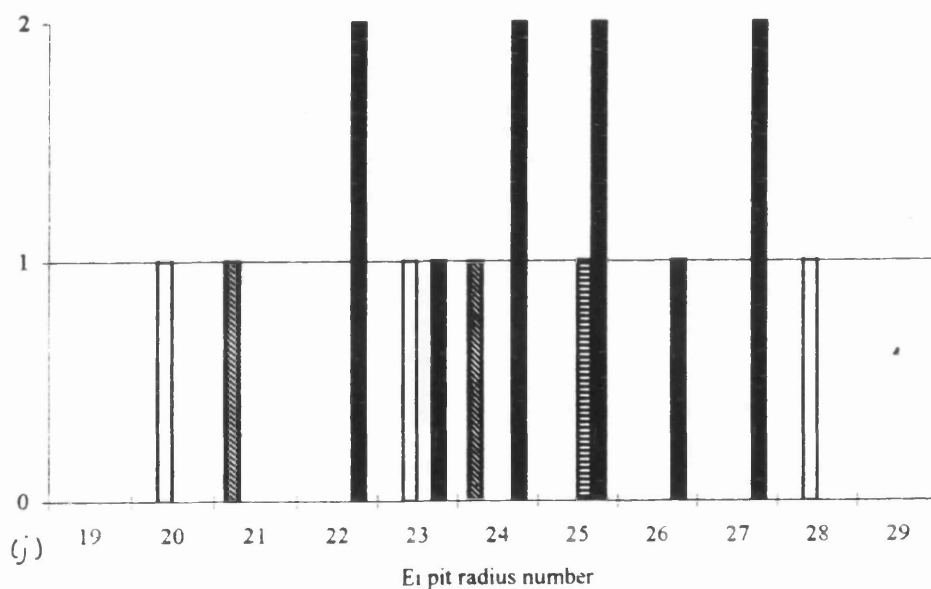
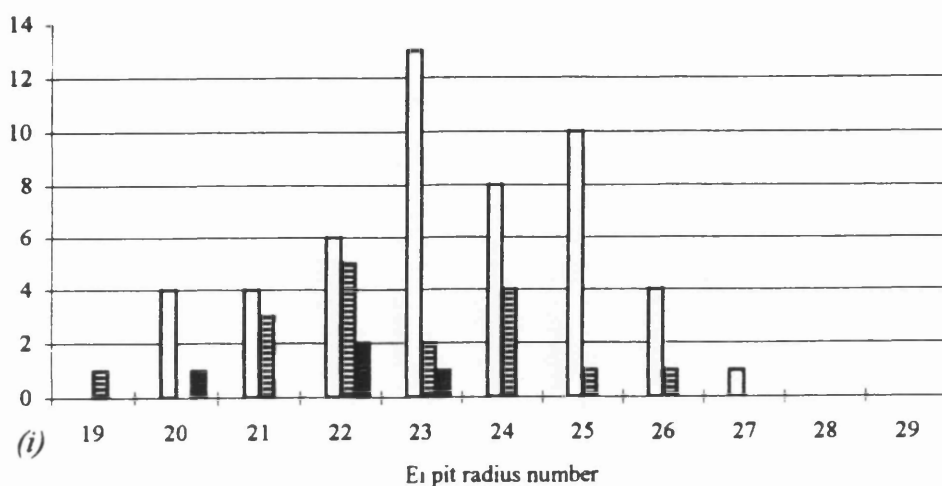


Fig. 5.3 Range and mean charts showing total pit count outside E1 arc for species as hitherto defined from (e) northern South Shropshire and (f) southern South Shropshire. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line.



harnagensis
 praecursor
 high E3 pit count specimen
 smeathenensis

Fig. 5.3 Frequency charts showing *I*₁ pit radius number for species as hitherto defined from early Harnagian of (g) northern South Shropshire and (h) southern South Shropshire.



harnagensis
 praecursor
 high E3 pit count specimen
 smeathenensis

Fig. 5.3 Frequency charts showing E1 pit radius number for species as hitherto defined from early Harnagian of (i) northern South Shropshire and (j) southern South Shropshire.

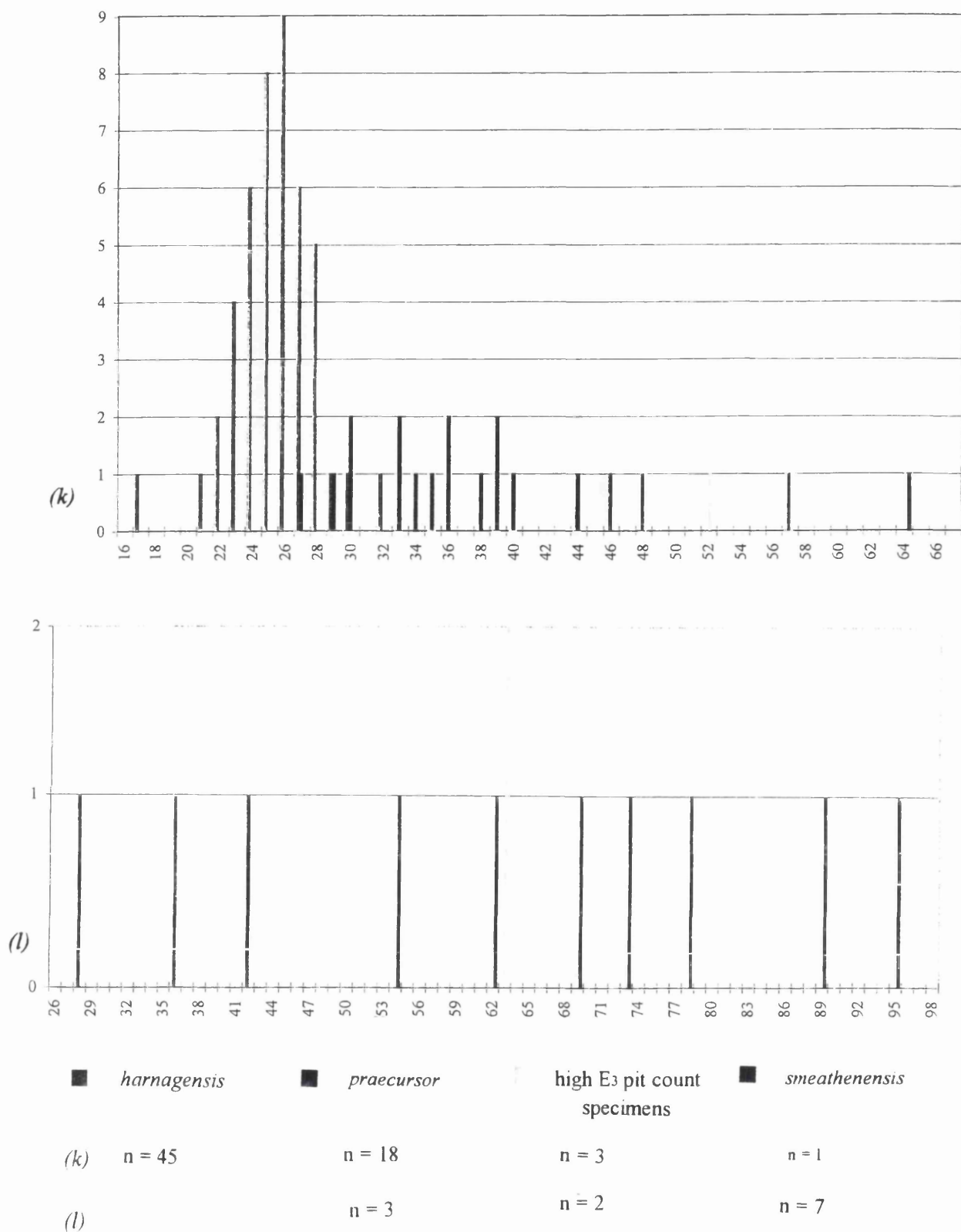


Fig. 5.3 Frequency charts showing total pit count outside E_1 arc for species as hitherto defined from early Harnagian of (k) northern South Shropshire and (l) southern South Shropshire.

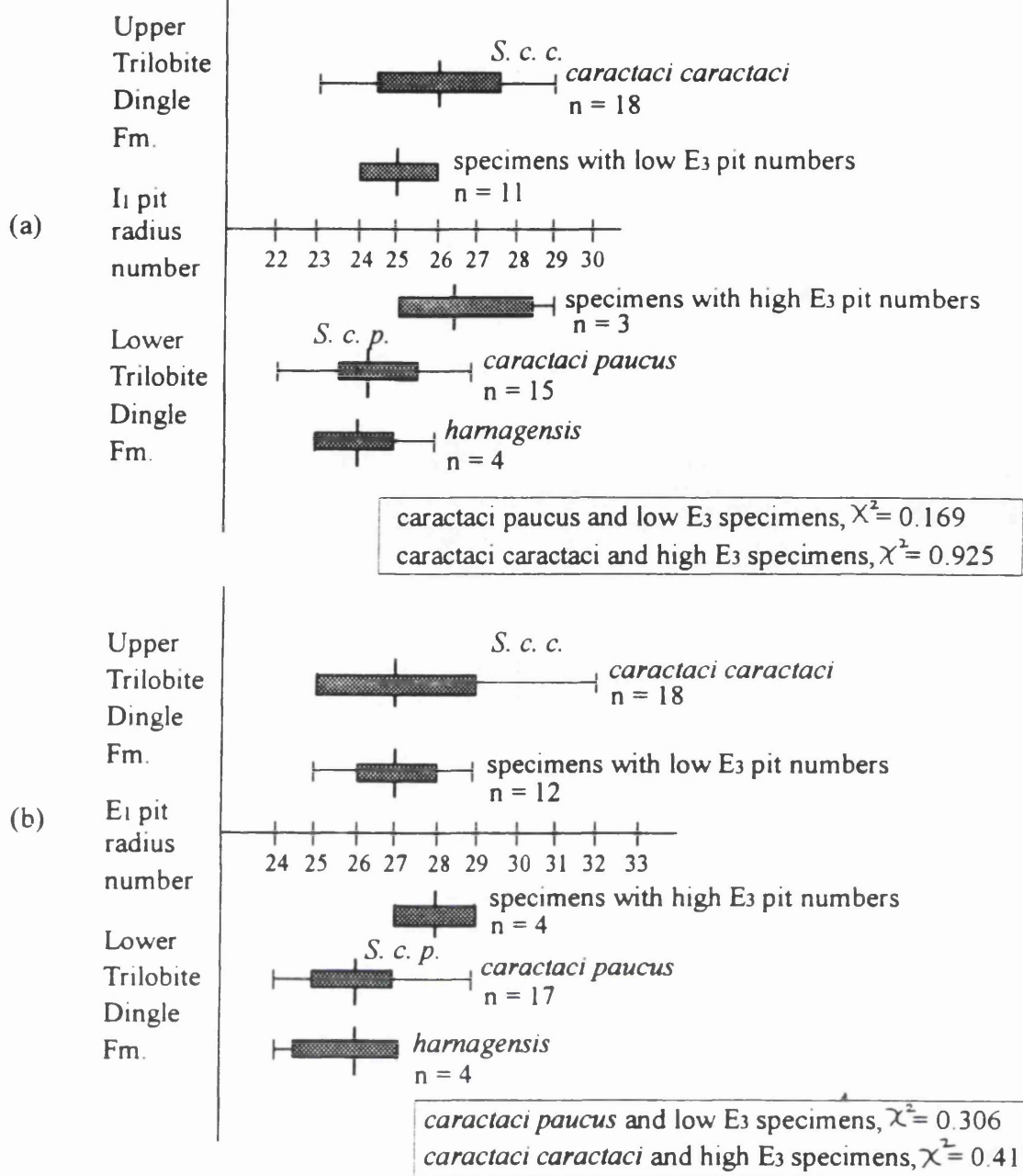


Fig. 5.4 Range and mean charts for species as hitherto defined showing (a) I₁ pit radius number for upper and lower Trilobite Dingle Shale Formation and (b) E₁ pit radius number for upper and lower Trilobite Dingle Shale Formation. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line. Box shows the chi squared test results.

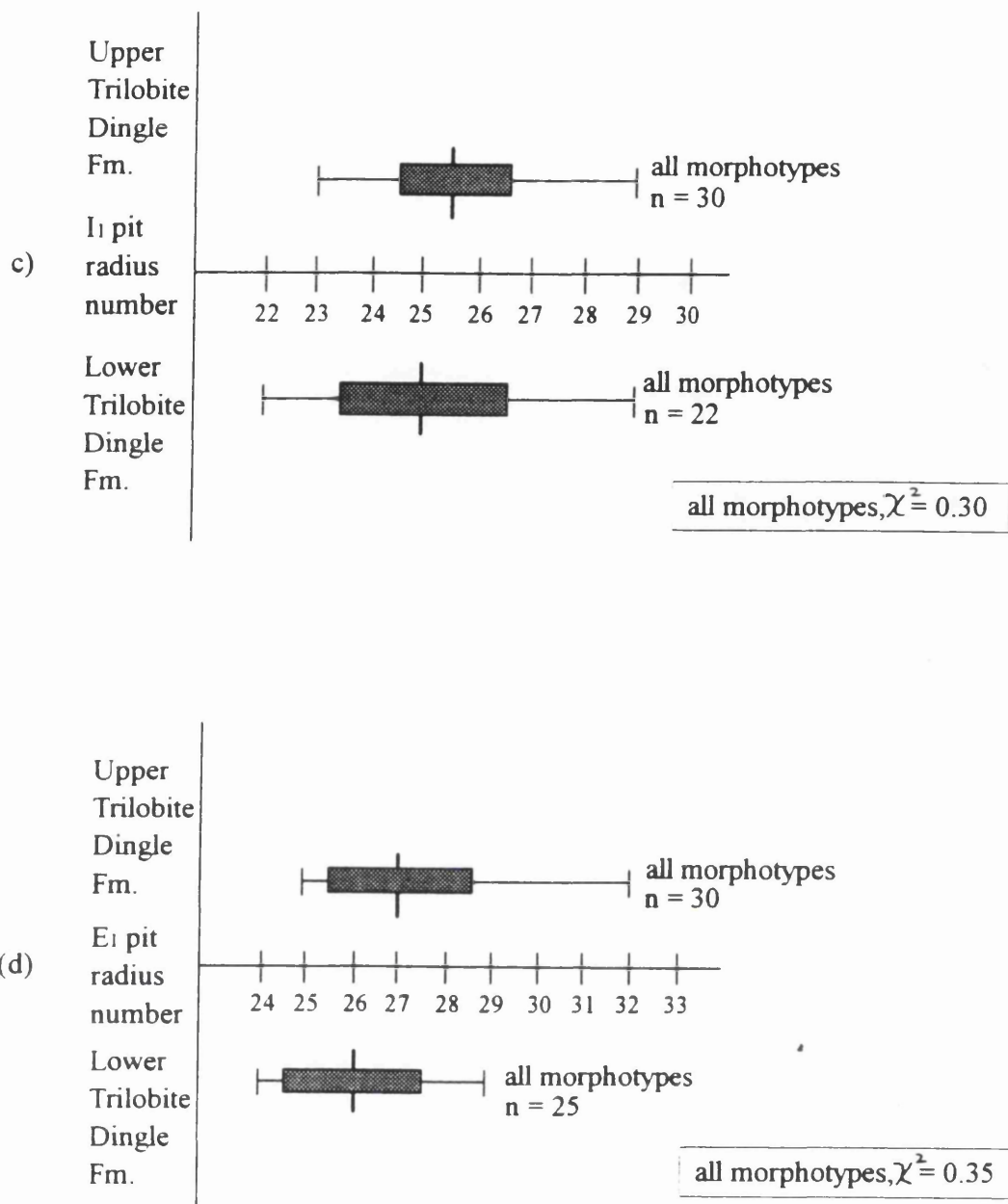


Fig. 5.4 Range and mean charts for each population showing (c) I₁ pit radius number for upper and lower Trilobite Dingle Shale Fm. and (d) E₁ pit radius number for upper and lower Trilobite Dingle Shale Fm. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. Box shows the chi squared test results.

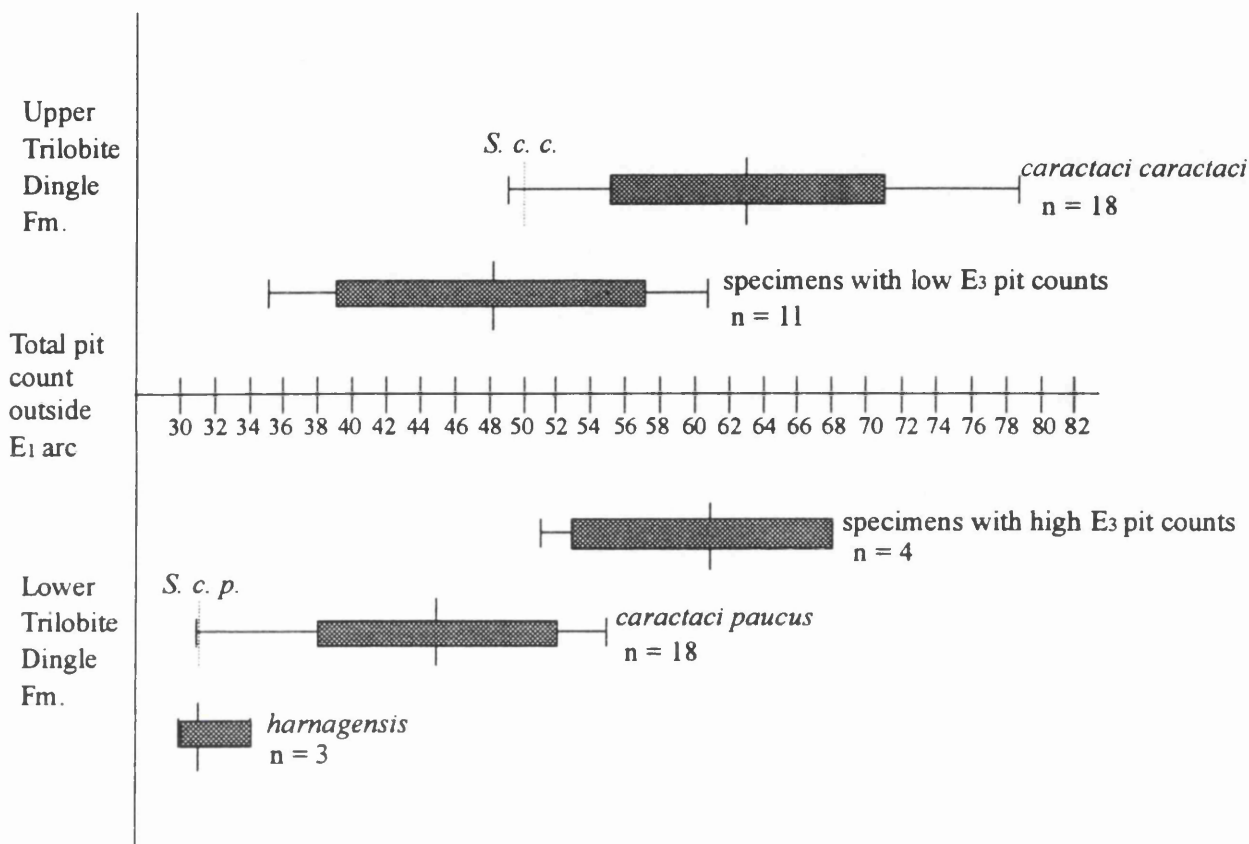


Fig. 5.4 (e) Range and mean charts for species as hitherto defined showing total pit count outside E₁ arc for upper and lower Trilobite Dingle Shale Beds. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line.

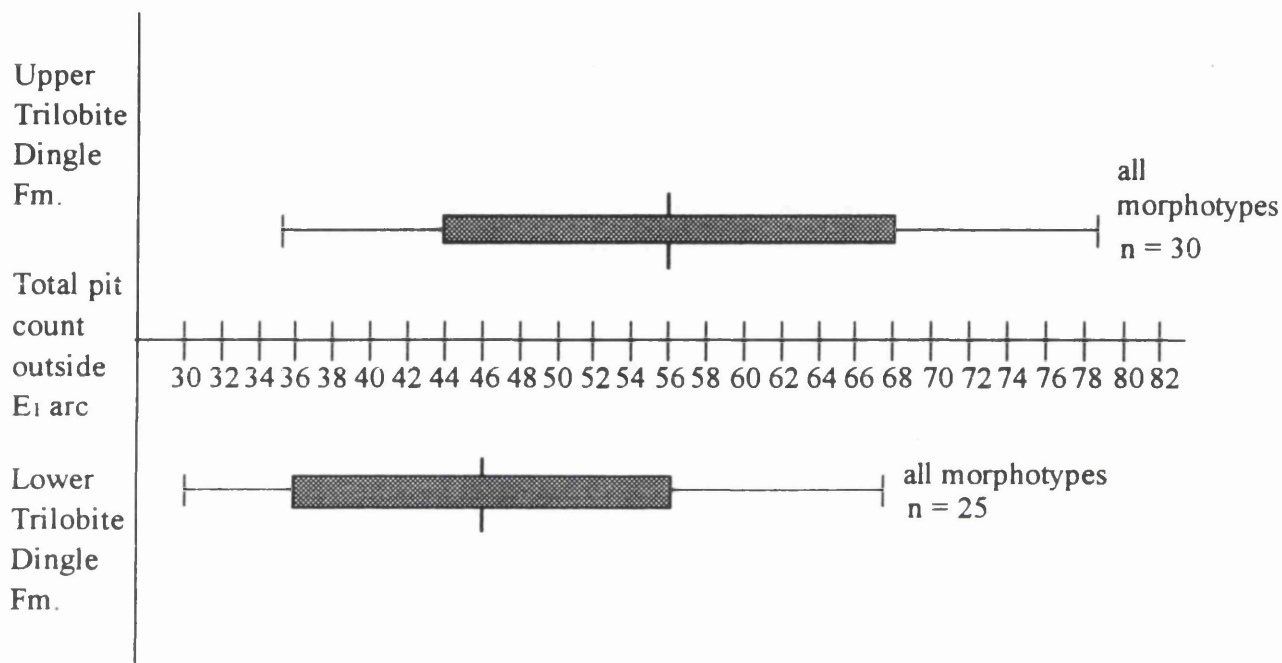


Fig. 5.4 (f) Range and mean charts for each population from upper and lower Trilobite Dingle Shale Beds showing the total pit count outside E₁ arc. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line.

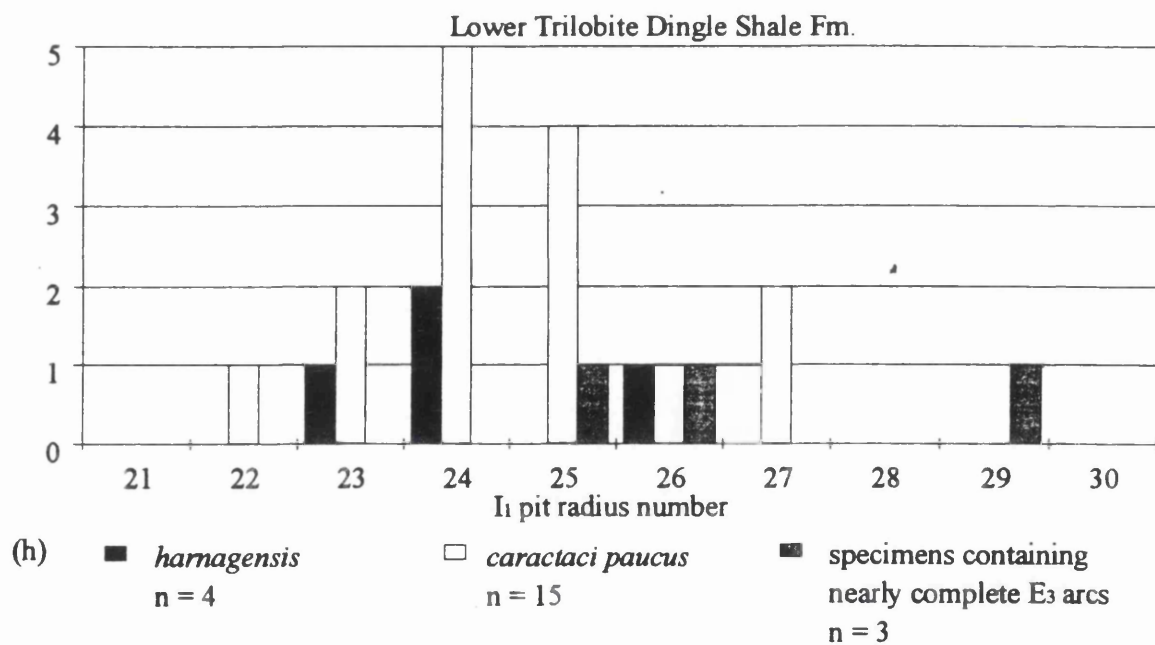
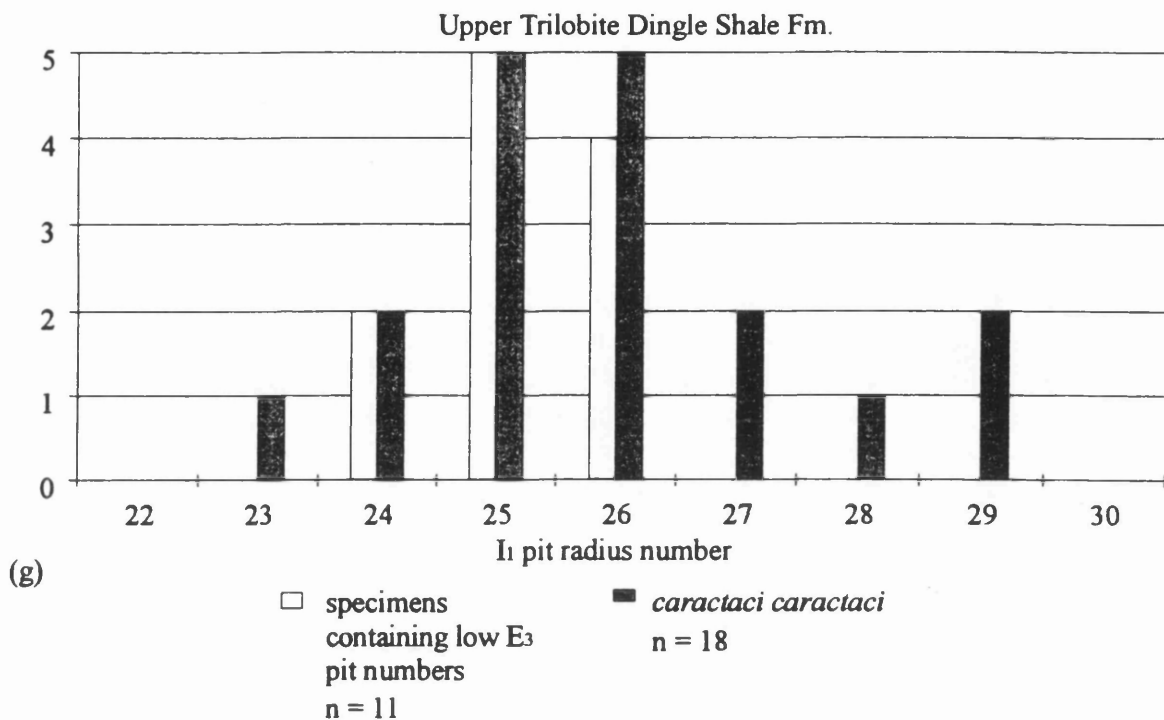


Fig. 5.4 Frequency charts showing I₁ pit radius number for species as hitherto defined from (g) upper Trilobite Dingle Shale Formation and (h) lower Trilobite Dingle Shale Formation.

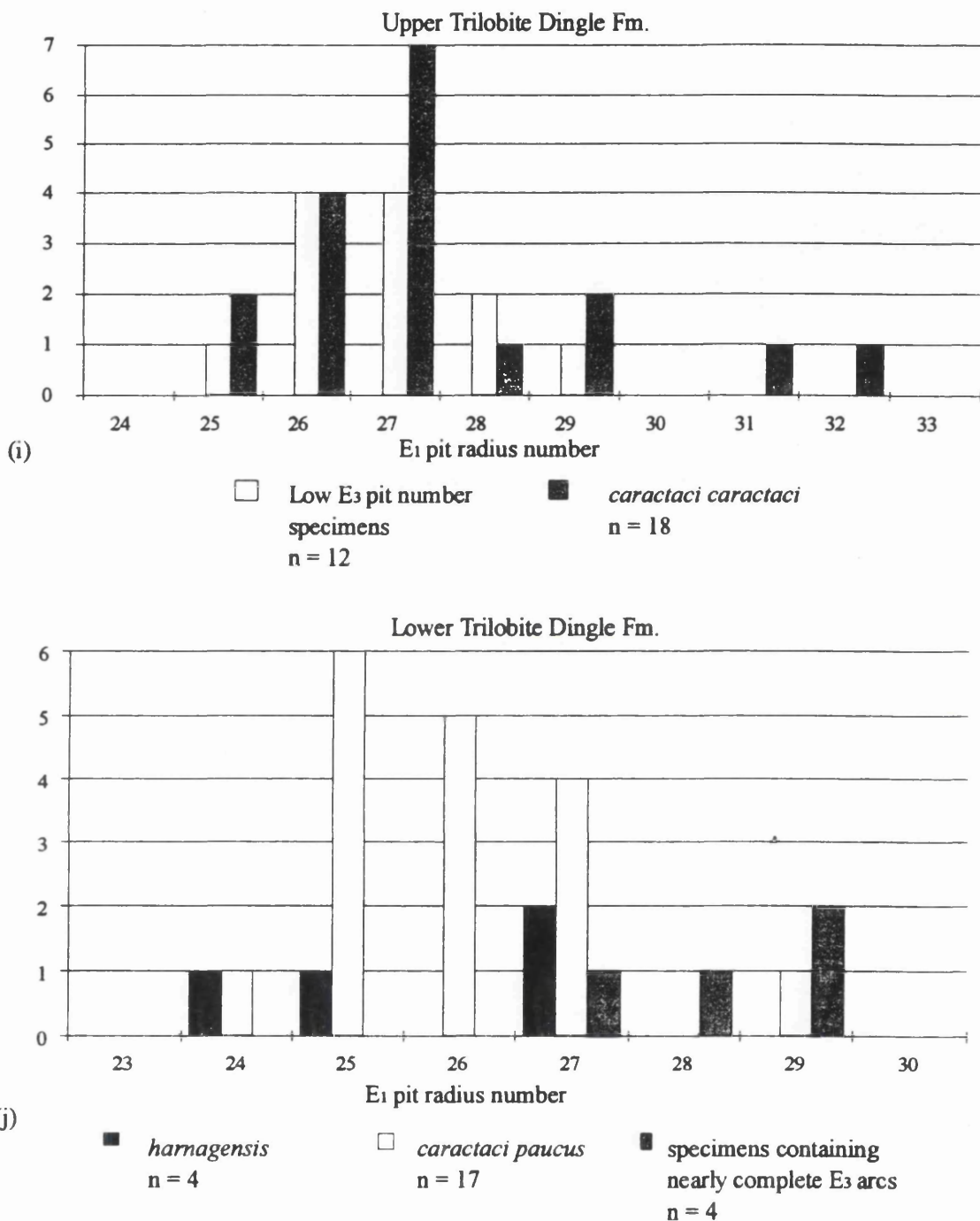


Fig. 5.4 Frequency charts showing E₁ pit radius number for species as hitherto defined from (i) upper Trilobite Dingle Shale Formation and (j) lower Trilobite Dingle Shale Formation.

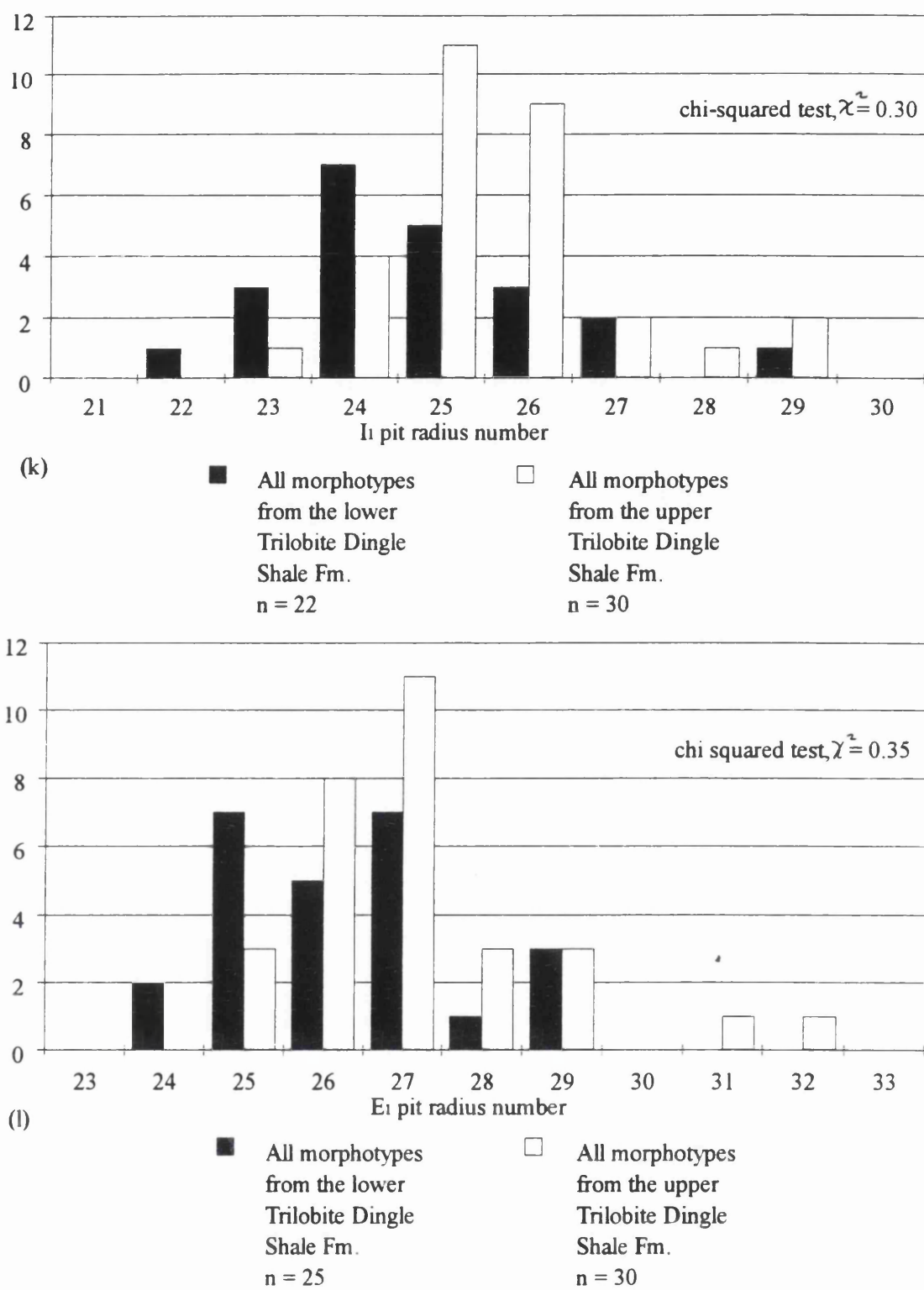


Fig. 5.4 Frequency charts showing (k) I₁ pit radius number for each population from upper and lower Trilobite Dingle Shale Formation and (l) E₁ pit radius number for each population from upper and lower Trilobite Dingle Shale Formation. The chi-squared test result is also shown.

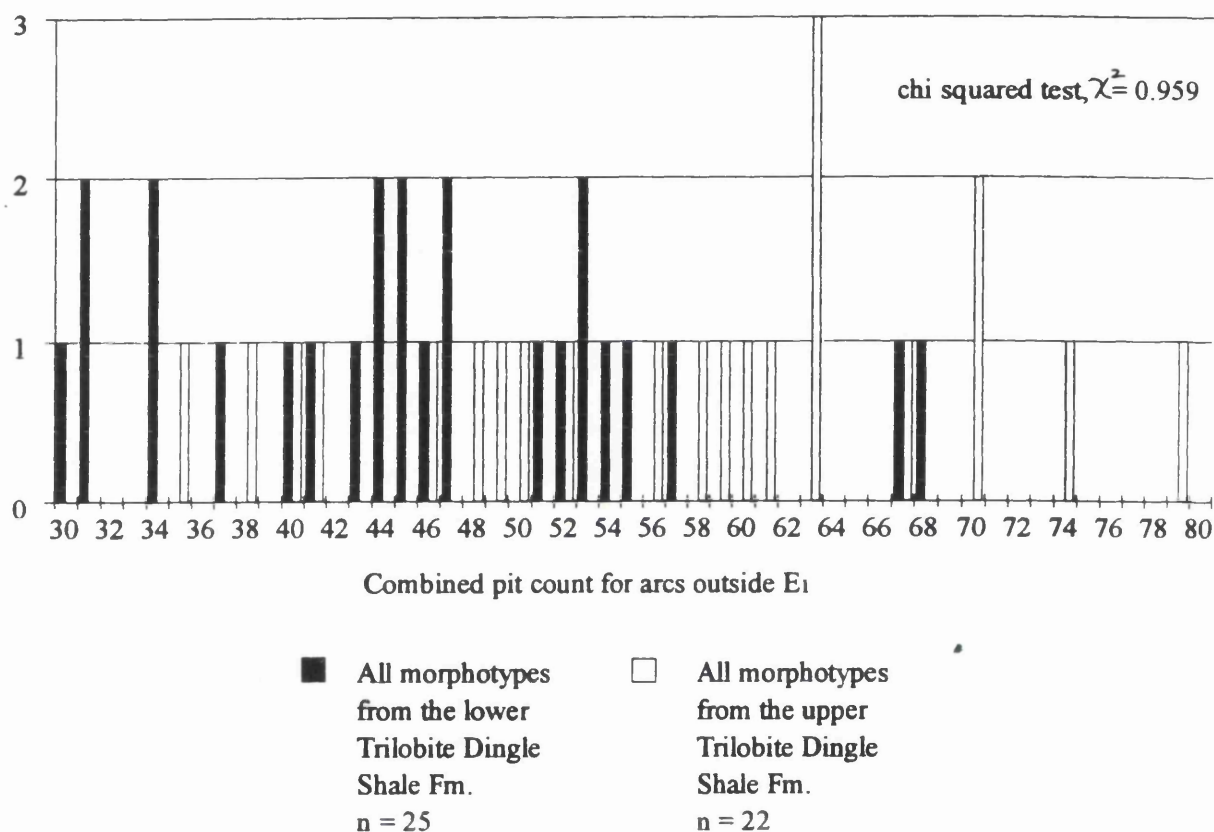


Fig. 5.4 (m) Frequency charts showing combined pit count outside E1 arc for each population from upper and lower Trilobite Dingle Shale Formation. The chi-squared test result is also shown.

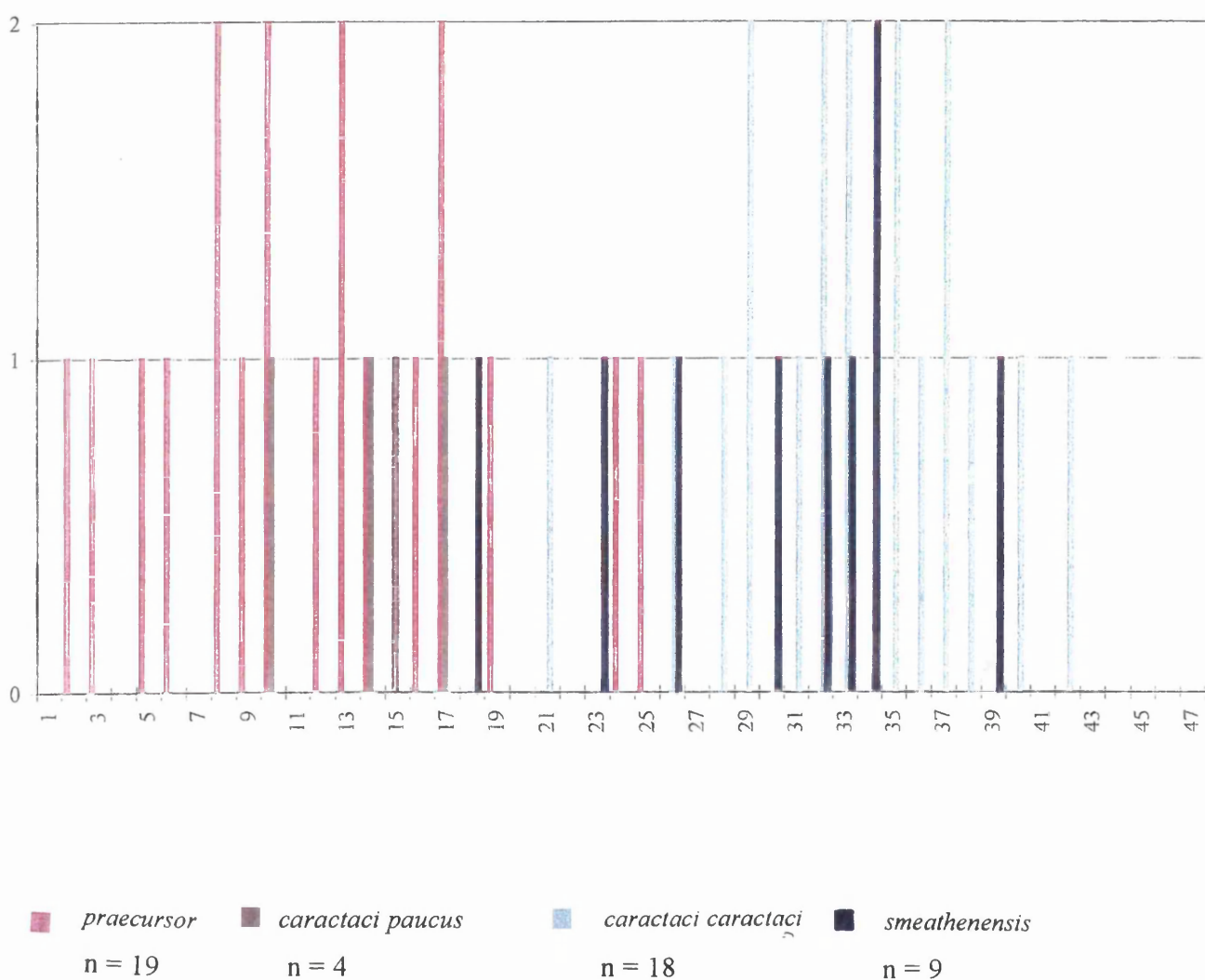


Fig. 5.4 (n) Frequency chart showing the E3 pit radius number for species as defined hitherto from their respective type localities.

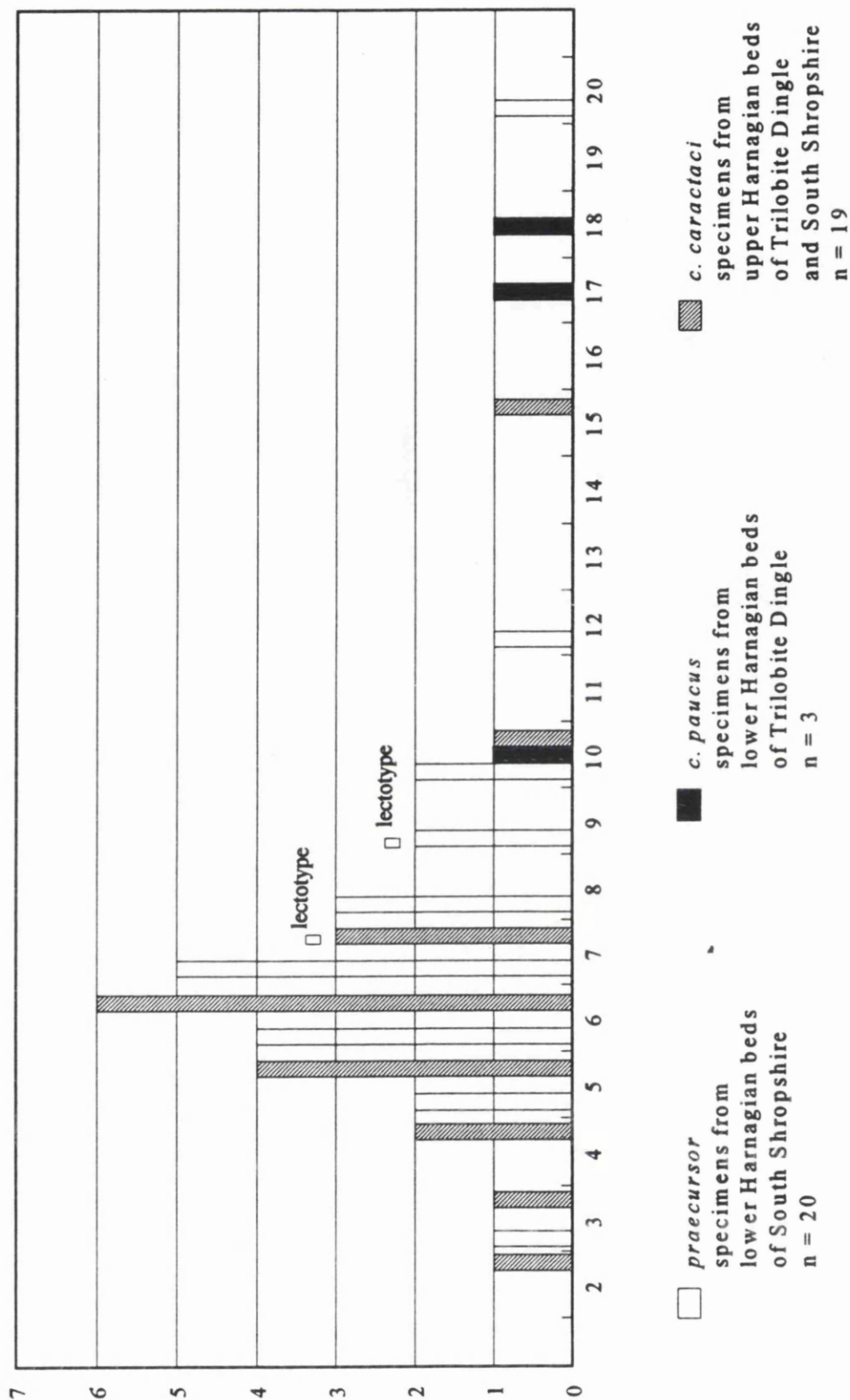


Fig. 5.4 (p) Frequency chart showing the termination position of the E_3 arc posteriorly with respect to the E_1 arc pits, for species as hitherto defined from their respective type localities.

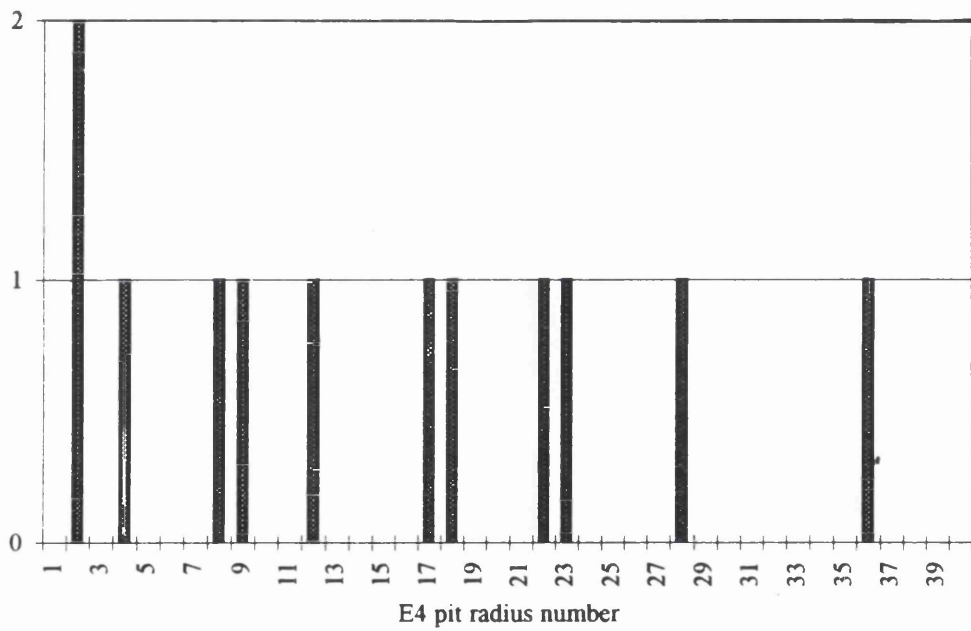


Fig. 5.4 (q) Frequency chart showing the *E4* pit radius number for *smeathenensis* as *hitherto* defined.

5.2 Harnagian - Soudleyan Boundary

The transition from Harnagian outer neritic shales of South Shropshire to glauconitic beds of early Soudleyan age marks the beginning of a marine regression (Hurst, 1979 and McKerrow, 1979). This led to the eventual disappearance of *caractaci caractaci* in the Soudleyan and to the emergence of forms more suited to this new environment. Taking advantage of the shallowing waters, a form similar in some respects to the earlier *harnagensis* appeared in the latest Harnagian. It had a similar fringe pit arrangement to the earlier morphotype except the E₂ pits were in radial alignment with I_n-E₁ pits and the radial rows produced are generally flexed forward. A few specimens show 2 or 3 extra E₂ pits anteriorly. Some also have slight radial ridges and a broader concentric band between I₁ and E₁ (Plate 2, Figs. 1 and 2).

This new arrival was recorded by Bancroft initially (1933) as a new genus *Ulricholithus*, then as a subgenus of *Salterolithus* (1949). Bancroft (1949) argued that *Ulricholithus* could not be regarded as an early *Broeggerolithus*, because of the lack of glabellar reticulation, the presence of strongly elevated radial ridges in E₁, increased body size and smaller modal pit numbers for I₁ arc. Whittard (1958) questioned Bancroft's reservations and proposed that *Ulricholithus* was synonymous with *Broeggerolithus* as a member of the group with well-developed E₁₋₂. Whittard noted one particularly interesting topotype specimen of "*Ulricholithus*" *ulrichi*, BM In 49710 (1958: plate 12, fig. 1), which appears to have well-developed radial ridges only on the right hand side of the fringe. This specimen was not available during the present study but another specimen (BM. In. 54024) also shows radial ridges only on one half of the fringe and does not appear to be tectonized (pers comm. A. W. Owen, 1994). Dean (1960) synonymised *Ulricholithus* with *Broeggerolithus* and suggested that *ulrichi* may be the link between *harnagensis* and *B. broeggeri* (Bancroft, 1929), the type species of *Broeggerolithus*, this view is supported here from the results detailed below.

The type locality of *ulrichi* is in the upper Harnagian Trilobite Dingle Formation of Middle House Dingle, north of Welshpool. The species is also found in the Glenburrell Fm. near Glenburrell Farm, Horderley, both these localities are in upper Harnagian rocks. Specimens from both localities contain individuals which

appear to conform to the typological view of *ulrichi* together with specimens which closely resemble *broeggeri* in having pronounced radial ridges, E₂ pits smaller than pits in the other arcs and the E₂ arc terminating before the genal angle is reached (see Plate 2, Fig. 3). The statistical results from this study seen in the charts of Fig. 5.5 show that *ulrichi* lies between *harnagensis* and *broeggeri* when considering their pit count means and ranges. Charts 5.5(a) and 5.5(b) show I₁ and E₁ arcs to have means within two pits of each other and ranges that significantly overlap for *harnagensis*, *ulrichi* and *broeggeri*. Chart 5.5(c) shows the greatest variation in pit ranges which is in the E₂ arc of the three forms, with the range of *harnagensis* taking in the full range of both *ulrichi* and *broeggeri*. As mentioned earlier (Section 5.1), the *harnagensis* E₂ arc ranges from specimens with well spaced pits giving low values on Chart 5.4(c) to those with a high density of pits almost producing a third E arc producing high values. These variations in E₂ pit content create the large variation seen in Chart 5.5(c). This explanation can also be used to some extent for the E₂ range in *ulrichi*. Chi-squared tests for the pit counts in the E₂ arc also show no significant difference between *ulrichi* and *broeggeri* at the 95 % confidence level. From the above observations Dean's (1960) proposal that there is a strong link between *harnagensis*, *ulrichi* and *broeggeri* is supported here.

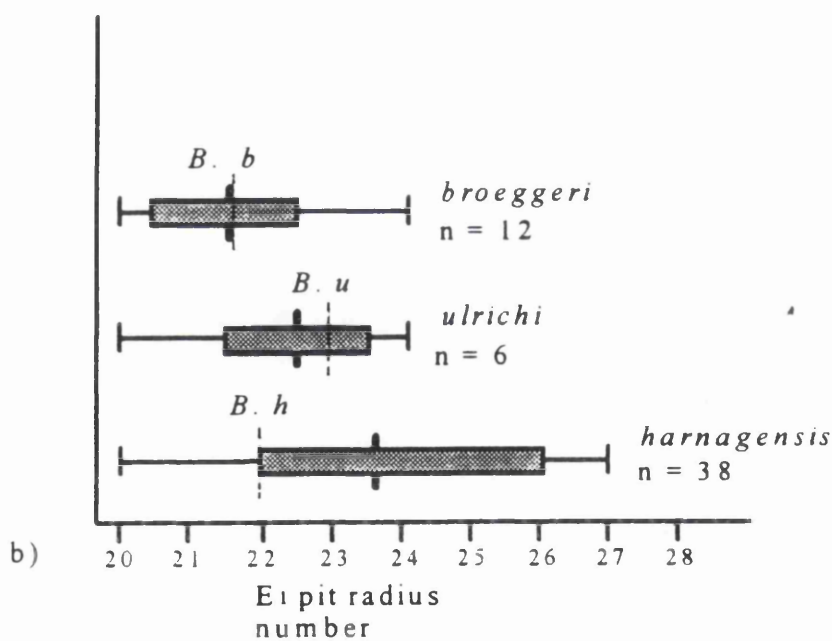
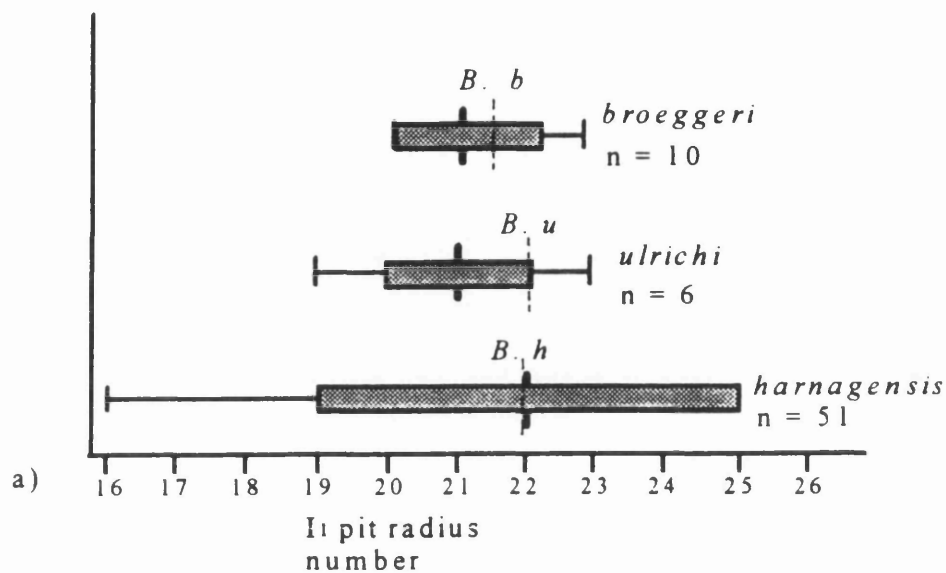


Fig. 5.5. Mean and range charts for *harnagensis*, *ulrichi* and *broeggeri* (as previously described) from their respective type localities. (a) I_1 arc pit radius numbers and (b) E_1 arc pit radius numbers.

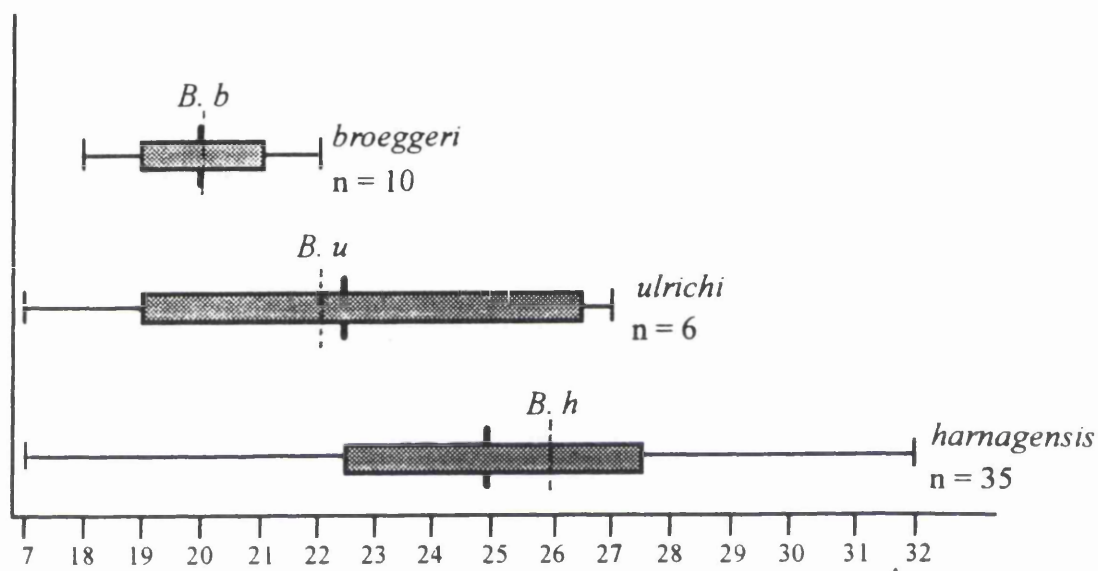


Fig. 5.5. (c) E_2 arc pit radius number mean and range charts for *harnagensis*, *ulrichi* and *broeggeri* (as previously described) from their respective type localities.

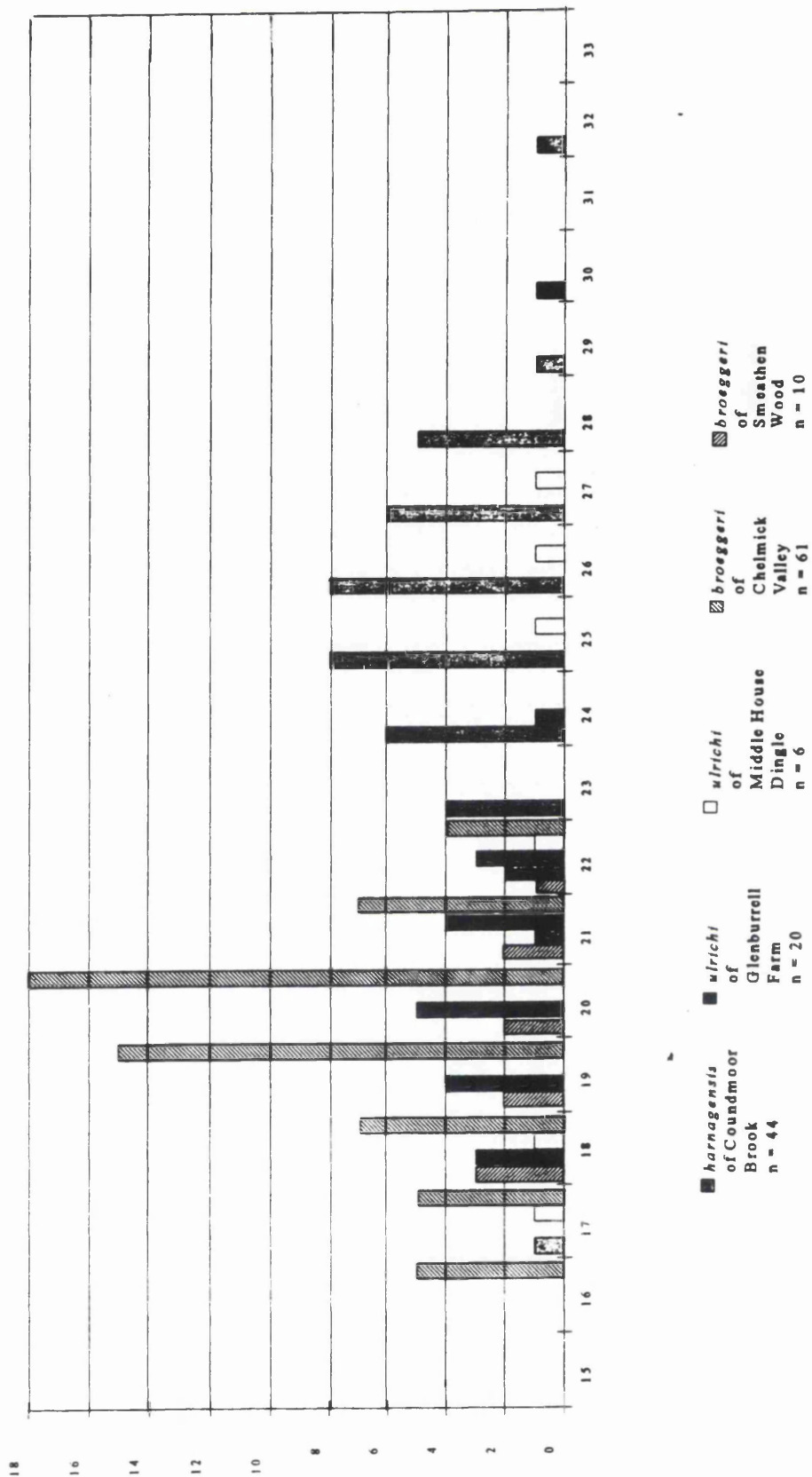


Fig. 5.5 (d) Frequency chart showing the E_2 pit radius number for *harnagensis*, *ulrichi* and *broeggeri* (as previously described) from localities noted in legend.

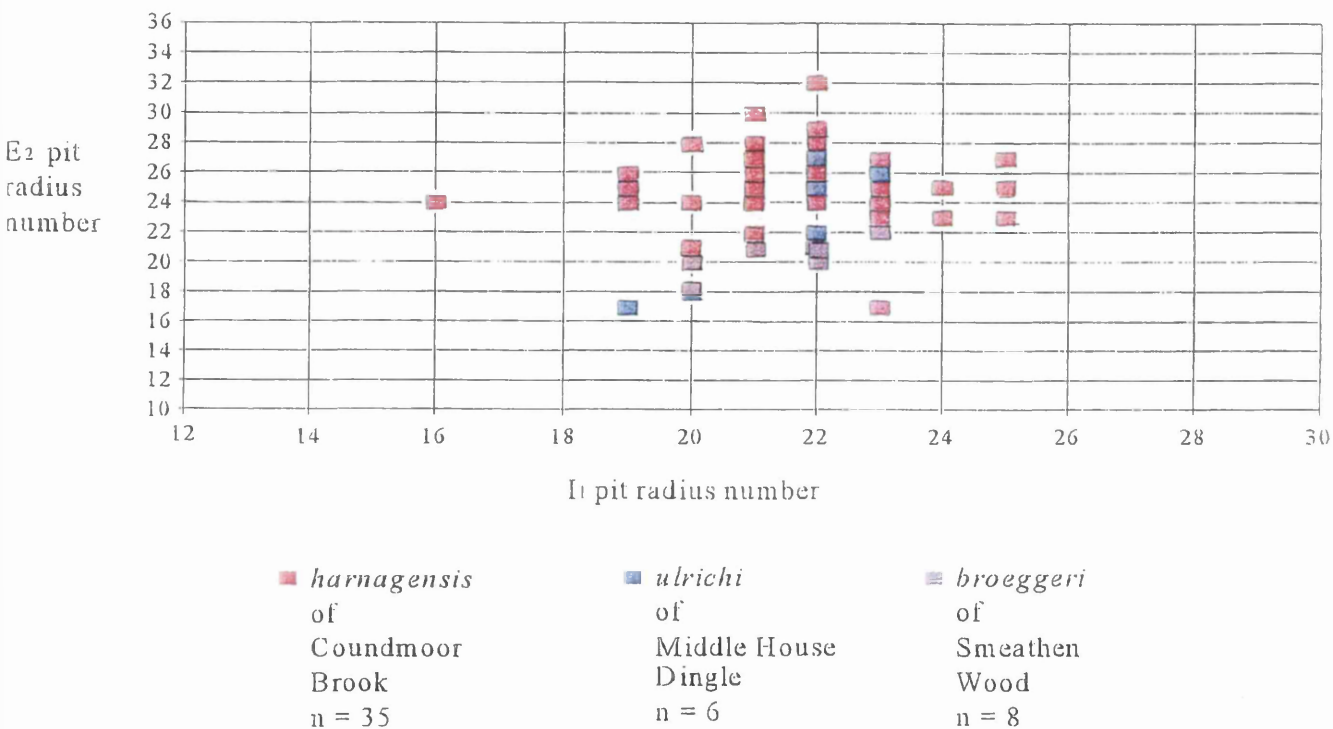


Fig. 5.5 (e) Chart showing I_1 pit radius number against E_2 pit radius number for *harnagensis*, *ulrichi* and *broeggeri* (as previously described) from localities noted in legend.

5.3 Soudleyan

The lower Soudleyan is dominated by *broeggeri*, the type species of *Broeggerolithus*, (type locality in the Glenburrell Formation, in the north-east corner of Smeathen Wood, near Horderley, Shropshire). It is found in beds assigned to the *B. broeggeri* Biozone in Shropshire, Welshpool, Shelve, the Berwyns Snowdon, Bala and Llansantffraid areas. It has distinct radial alignment of pits in all four arcs and has prominent radial ridges, which commonly extend from the I_1 arc to the E_2 arc; the angular cephalic outline is the result of the pits being small anteriorly and pits of E_1 and I_1 increasing in size posterolaterally. Bancroft (1929a) stated that the specific name was not to be applied to specimens unless all or nearly all of them in a sample exhibited intercalated E pits in front of the glabella, even though specimens lacking this feature might resemble *broeggeri* in other respects. This led to many specimens, including some from the type locality being excluded by him and subsequent authors. Dean (1960) questioned the confining limits of the species but remained cautious, terming some specimens *B. cf. broeggeri* (Plate 2, Fig. 4). This restrictive view of the species is unworkable as specimens from the same sample appear the same in all characteristics except their mesial pit patterns (see below). In this study, specimens are grouped as *broeggeri* if all or nearly all the criteria are satisfied without attention to the mesial pit arrangement.

A locality in the lower Soudleyan Chatwall Flags in the Chelmick Valley, near Soudley, northern South Shropshire, has yielded a large sample of some 150 well preserved specimens. Whilst showing most of the characteristics of *broeggeri* there is a great variety of mesial pit pattern (see Fig. 5.6). The specimens show six main categories of mesial pit pattern (a)-(f) and over half of the specimens show intercalated (auxiliary) pits (pits not fitting exactly into a concentric arc), which Bancroft specified as a major criterion for *broeggeri* (Bancroft 1929a). The majority of specimens, 58% of the population sample, group (c) in Fig. 5.6, have one E_1 pit on the sagittal line only, more ordered varieties (a) and (b) similar mesial pit patterns to those of *ulrichi* are present (17% combined). The groups (d), (e) and (f) show E_2 pits being radially spaced further from the mesial line by addition of more rows or single E_1 pits mesially (25% combined). These last types are very similar to

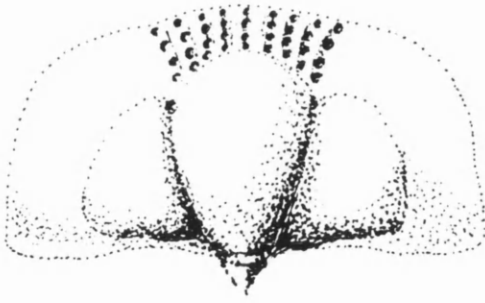
soudleyensis, of late Soudleyan age (see below). These pit patterns appear to illustrate variation within one interbreeding population.

B. constrictus Bancroft, 1949 was described as a rare species found with *broeggeri*. Its type locality is at the base of the Soudleyan Stage, in the stream section west of Ceunant, Welshpool. It is recognised by a constriction of the posterior part of one or more outside arcs. This feature is very similar to that seen in some specimens of *broeggeri*, this constriction may be due to injury during ecdysis and one extreme case is found in a specimen of *B. transiens* of Marshbrookian age (see Section 5.6 and Plate 2, Figs. 4, 5 and 10). It is considered here that *constrictus* is synonymous with *broeggeri*.

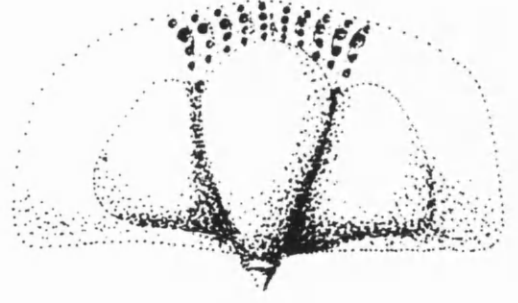
B. soudleyensis (Bancroft, 1929a) (type horizon and locality: the late Soudleyan Chatwall Sandstone, in Soudley Quarry, Shropshire) replaces *broeggeri* as the dominant form and becomes the zonal trilobite for the upper Soudleyan. It resembles *broeggeri* morphologically in all respects except for its more limited E_2 arc, which is absent anteriorly and posteriorly. Statistically there is a two pit difference between *broeggeri* and *soudleyensis* in terms of their I_1 arc mean pit counts and less than one pit difference in their E_1 arc mean pit counts (see Fig. 5.7). Their ranges of variation for the I_1 and E_1 arcs also overlap, the shift to lower values seen in *soudleyensis* may be a reflection of the shallowing of the environment (Hurst, 1979; McKerrow, 1979). The absence of E_2 pits anteriorly and posteriorly in *soudleyensis* is shown in Fig. 5.7(c) with a low range of pits. It may be significant that the E_2 range in *broeggeri* follows on from that of *soudleyensis* with no break but a larger sample would be needed to confirm this trend.

In the lower Soudleyan, specimens conforming to *soudleyensis* are found with *broeggeri* (s. s.) in the Chelmick sample (see above) and an extreme individual with only 6 pits laterally in E_2 (see Pl. 2, Fig. 6) was found in the uppermost Smeathen Wood Formation of early Soudleyan age, in the north-east corner of Smeathen Wood, Shropshire. Previous authors have also noted rare forms of *soudleyensis* in lower Soudleyan samples of *broeggeri* and *caractaci caractaci* (Bancroft 1935; Whittard 1957 and Dean 1960). This would suggest that *soudleyensis* emerged as a variant of *broeggeri* and became dominant in the late Soudleyan possibly due to its better adaptation to the changing environment. From the evidence shown above it is

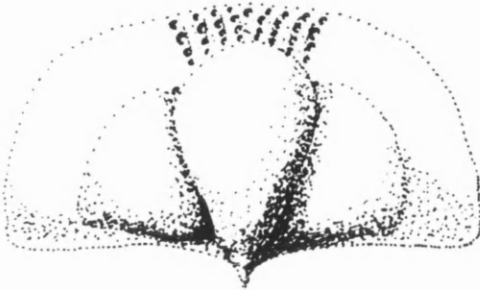
proposed that there are insufficient morphological differences to warrant keeping *ulrichi*, *constrictus* and *soudleyensis* separate at species level and that they should be classified closer to *broeggeri*. This then raises the problem as to when *broeggeri* and *soudleyensis* diverged sufficiently to isolate *soudleyensis* as a temporal subspecies of *broeggeri*, this will be addressed in the next Chapter 6.



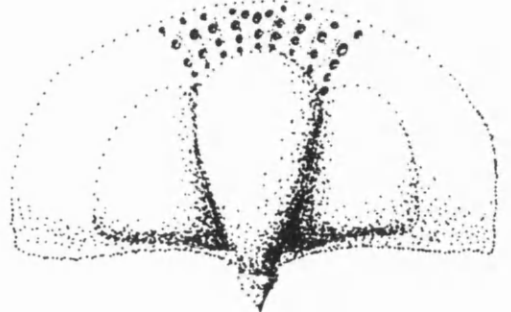
(a)
13%
n = 9



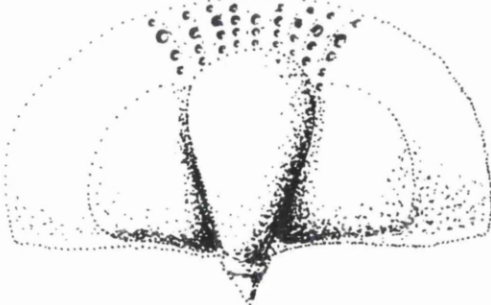
(b)
4%
n = 3



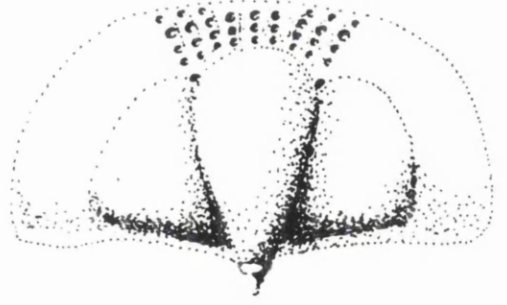
(c)
58%
n = 42



(d)
17%
n = 12



(e)
3%
n = 2



(f)
5%
n = 4

Fig. 5.6. Sketches showing the variations in the mesial pit pattern of specimens in a single population of *broeggeri* from the lower Soudleyan Beds at Chelmick Valley, Shropshire. The sample total = 72. Scale approximately $\times 4$.

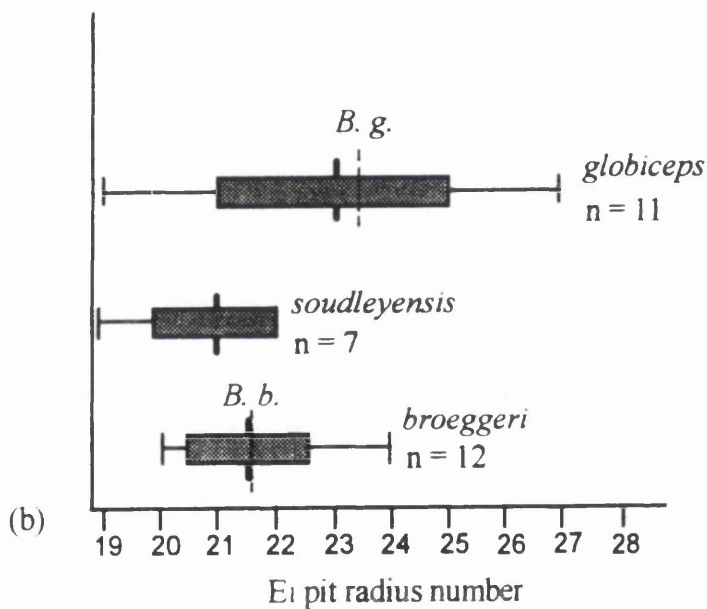
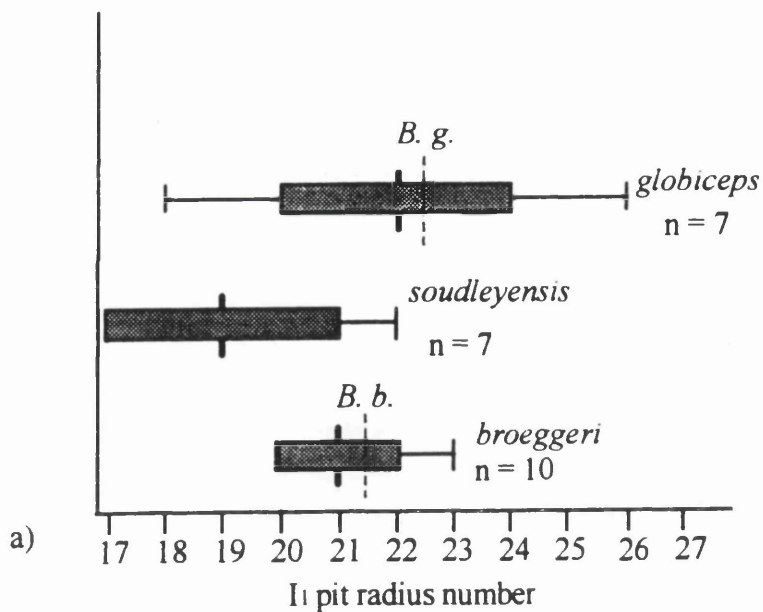


Fig. 5.7. Mean and range charts for *broeggeri*, *soudleyensis* and *globiceps* (as hitherto described) from their respective type localities except for *globiceps* which also contains all specimens from its other locality to increase the sample number. The lectotypes of *broeggeri* and *globiceps* are displayed as vertical hatched lines. The lectotype of *soudleyensis* does not contain complete I₁ or E₁ arcs. (a) I₁ pit radius numbers. (b) E₁ pit radius numbers.

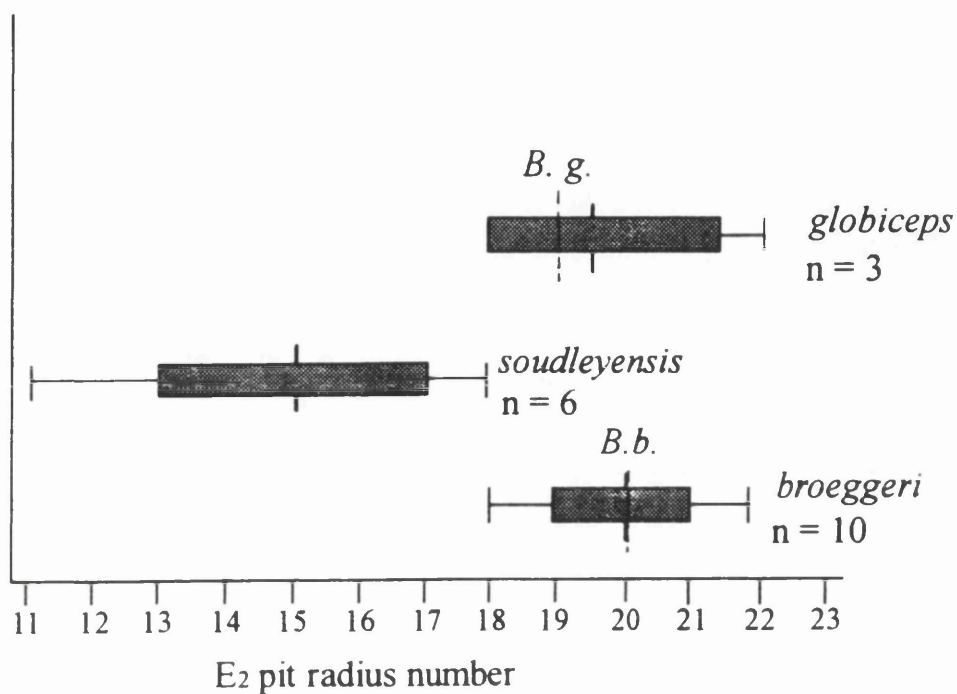


Fig. 5.7 (c) Mean and range chart for E_2 pit radius number of species as hitherto defined from their respective type localities except for *globiceps* which also contains all specimens from its other locality to increase the sample number. The lectotypes of *broeggeri* and *globiceps* are displayed as vertical hatched lines. The lectotype of *soudleyensis* does not contain a complete E_2 .

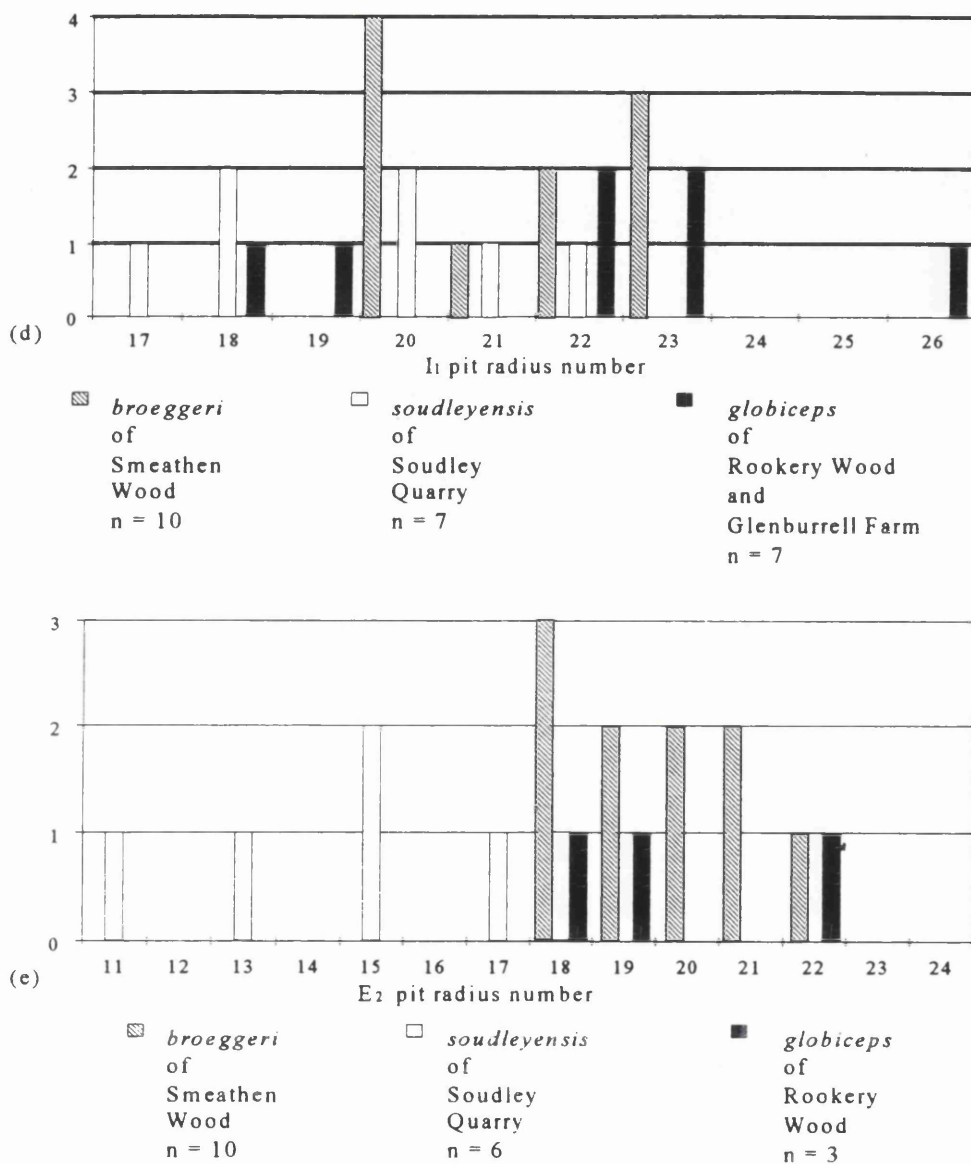


Fig. 5.7 Frequency charts for species as hitherto defined from their respective type localities except for *globiceps* which also contains all specimens from its other locality to increase the sample number. Showing (d) I1 pit radius number and (e) E2 pit radius number.

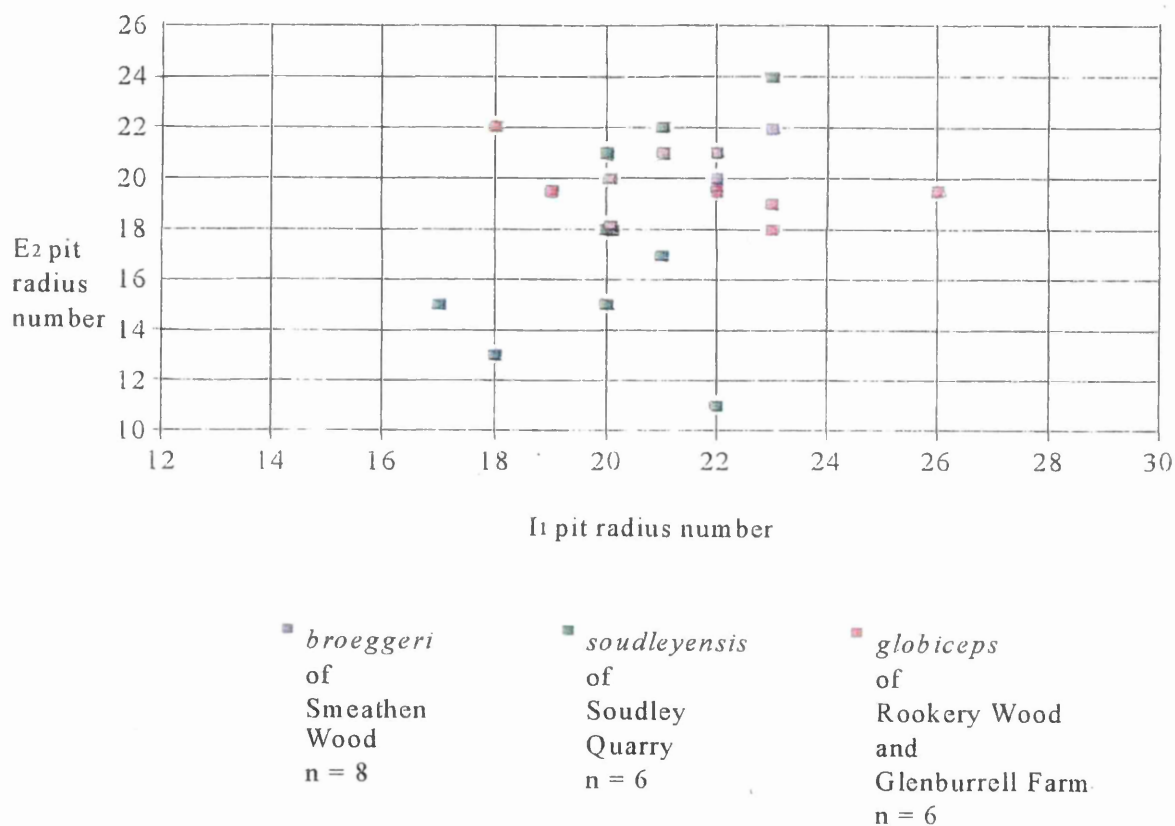


Fig. 5.7 (f) Chart showing I1 pit radius number against E2 pit radius number for species as hitherto defined. Specimens are from the respective type localities except for *globiceps* which also contains all specimens from its other locality to increase the sample number.

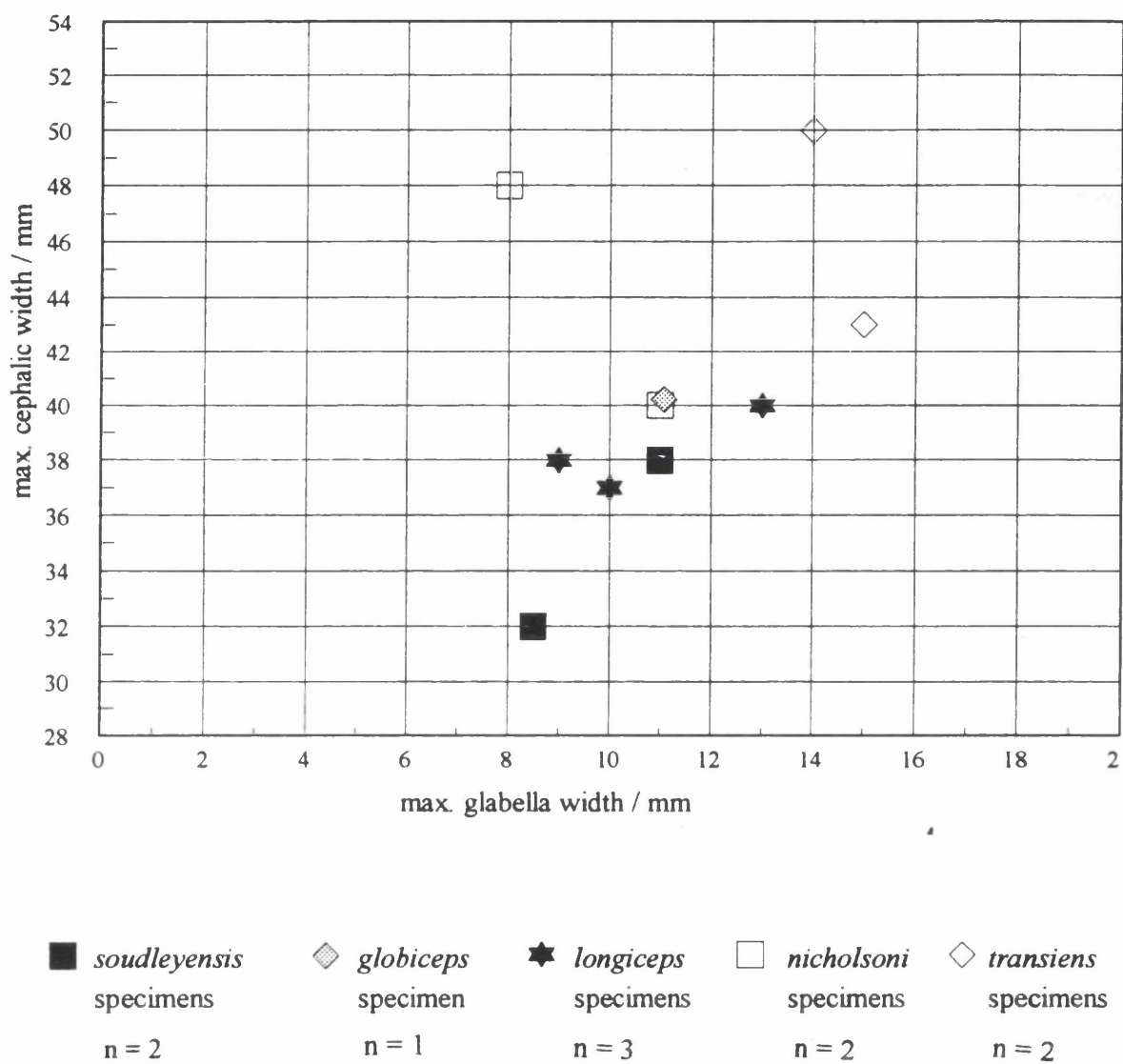


Fig. 5.7 (g) Chart showing maximum width of the glabella (mm) against maximum width of the cephalon (mm) of undistorted specimens from species as hitherto defined.

5.4 Longvillian

In southern South Shropshire as a marine transgression began (Hurst, 1979; McKerrow, 1979) a form termed *B. globiceps* (Bancroft, 1929) appeared in the *Dalmanella leptota* and *indica* biozone. This form occurs in the Horderley Sandstone Formation and shows a close resemblance to *broeggeri* and *soudleyensis* with its radial alignment of pits, radial ridges and broad concentric lists posterolaterally. Its type horizon and locality is the upper Horderley Sandstone Formation (*Dalmanella leptota* Biozone) in the south western corner of Rookery Wood, Horderley, Shropshire. It has been distinguished in the past by its longer, more rounded cephalon, conspicuous, tumid glabella and by the absence of some pits of E₂ in front of the glabella. The large glabella is the most significant feature which differentiates *globiceps* from *broeggeri* and *soudleyensis*. However some specimens of *globiceps* are remarkably similar morphologically to *broeggeri* (Plate 2, Figs 7 and 8). Chart Fig. 5.7 (g) compares the glabella and cephalon sizes of undistorted specimens from different species. There appears to be very little difference between the species although larger samples would give a more accurate result.

Statistical results displayed in the charts of Fig. 5.7 show the mean pit counts of *broeggeri* and *globiceps* differ by a maximum of two pits and the range of variations in pit counts overlap considerably. These results would tend to suggest that *globiceps* may be another geographical and temporal variant of *broeggeri*.

Dean (1960) erected *B. simplex* on one specimen from the type locality of *globiceps*. In a later publication (1962) he synonymized *simplex* with *B. nicholsoni* (Reed, 1910). The species *nicholsoni* (type horizon and locality, the Lower Melmerby Beds of the Alston Road cutting, near Melmerby, Cumbria and the species is also present in the Longvillian of the Cross Fell area and South Shropshire) has a simple fringe, a rounded cephalic outline, no radial ridges, the equally-sized radially aligned pits appear to be in sulci anteriorly on the upper lamella in some specimens and posteriorly I_n and I₁ arc pits become large and inhibit the continuation of radial rows (Plate 2, Fig. 9). Morphologically there are significant differences between *nicholsoni* and contemporaneous *globiceps*, for example, radial ridges, pit size variation and cephalic outline. Statistically, however, they do appear very similar. The mean pit counts vary by one pit and the range of variations overlap considerably

for all three arcs (see Figs. 5.7 and 5.8). In a work by the British Geological Survey (B.G.S) on the Dufton Shales of the Cross Fell area *globiceps* and *longiceps* were considered subspecies of *nicholsoni* (Burgess and Holliday, 1979). The *globiceps* synonymy is disputed here as there are sufficient morphological differences between the two forms (see also Chapter 6). In the same work it was noted that both *longiceps* and *globiceps* occurred together. Dean (1991) described *nicholsoni* specimens from the Longvillian Oxhe Formation, Le Petit Fond d'Oxhe, Belgium. Dean noted that good radially aligned pits extended to the anterolateral position in the poorly preserved and distorted specimens. Specimens conforming to *nicholsoni* are also found in Ireland, see Section 5.8.

5.5 Woolstonian

The base of the Woolstonian is marked by the Alternata Limestone which succeeds the Horderley Sandstone Formation in southern South Shropshire and disconformably overlies the Soudleyan Chatwall Sandstone in northern South Shropshire. It was only from this limestone horizon that *B. longiceps* (Bancroft, 1929) was recorded until the recent work by the B. G. S. in the Dufton Shales of the Cross Fell area (Burgess and Holliday, 1979). The type locality of *longiceps* is in a small stream by the west side of the road from Horderley to Marshbrook, north of Whittingslow, Shropshire. Morphologically *longiceps* is closely allied to *nicholsoni* with its more rounded cephalic outline, E₂ pits are present mesially, pits of all arcs are of equal size anteriorly, radial ridges are present on a small scale in a few specimens, and radial lists become broader anteriorly and I_n and I₁ arc pits become larger posteriorly. The glabella appears longer than that of *nicholsoni* in some specimens but measurements made on undistorted specimens show no significant differences see Fig. 5.7(g). Statistically there is also no significant difference in the mean pit counts and ranges of variation of *longiceps* and *nicholsoni* (see Fig. 5.8). It is therefore proposed here that *longiceps* is synonymized with *nicholsoni*. Dean (1962) remarked on the similarities of the two species but stated that no specimens of *nicholsoni* have been found with auxiliary pits in E₂ unlike *longiceps* and hence retained both species. A specimen of *nicholsoni* has since been discovered in the Dufton Shales showing numerous E₃ pits anterolaterally, see Plate 2, Fig. 11. Rushton in the B. G. S. sheet

memoir of Brough-under-Stainmore (Burgess and Holliday, 1979) considered *longiceps* a subspecies of *nicholsoni*. The B.G.S. used the two "subspecies" *nicholsoni globiceps* and *nicholsoni longiceps* as the main aid to dating certain beds in the Cross Fell area (Burgess, 1979), however they also pointed out difficulties in distinguishing between the two "subspecies". The view here is that there are sufficient differences between "*globiceps*" and "*longiceps*", and "*longiceps*" is synonymous with *nicholsoni*, which is contemporaneous with "*globiceps*".

B. melmerbiensis (Dean, 1962) is based on one large specimen from a loose nodule of impure limestone in the Alston Road cutting, north-east of Melmerby in the Cross Fell district. Its pit counts fall well within the range of *nicholsoni* (see Fig 5.8) and has similar fringe characteristics. This specimen probably represents a rather long-lived and hence large *nicholsoni* individual.

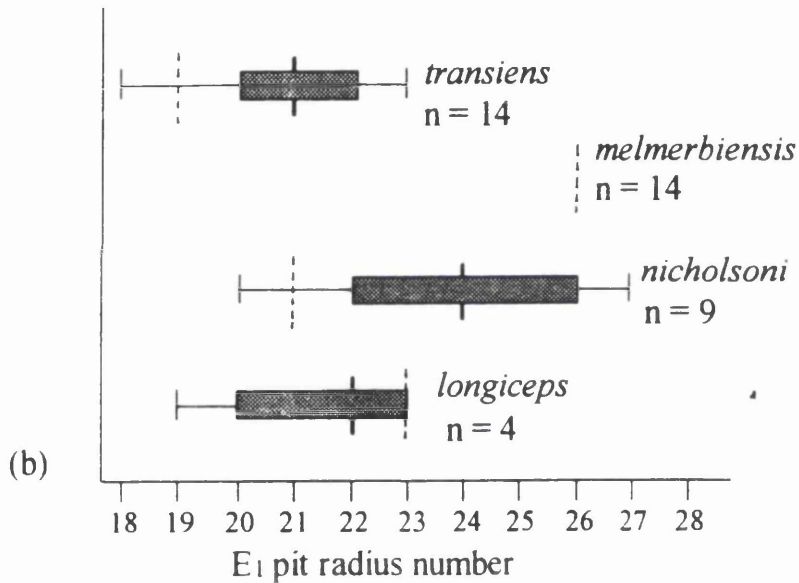
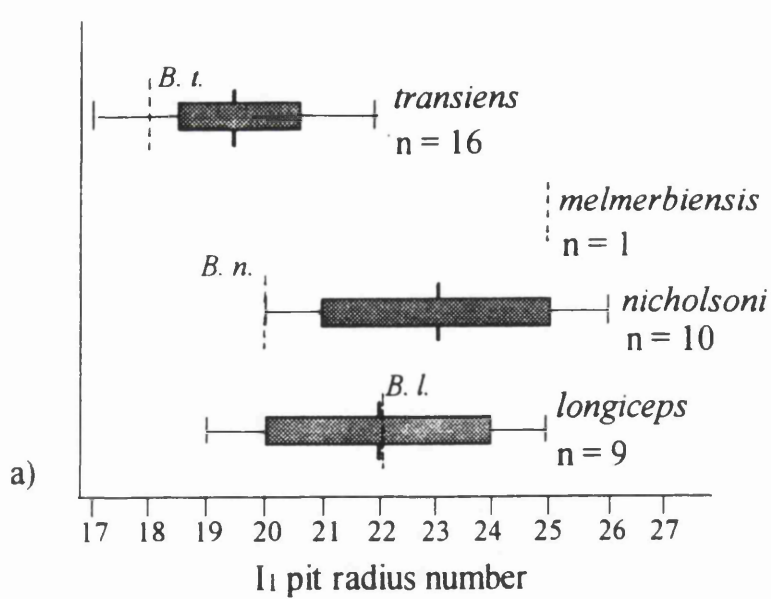


Fig. 5.8 Range and mean charts for species as hitherto defined showing (a) I₁ pit radius number and (b) E₁ pit radius number. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line. Samples are from more than one locality.

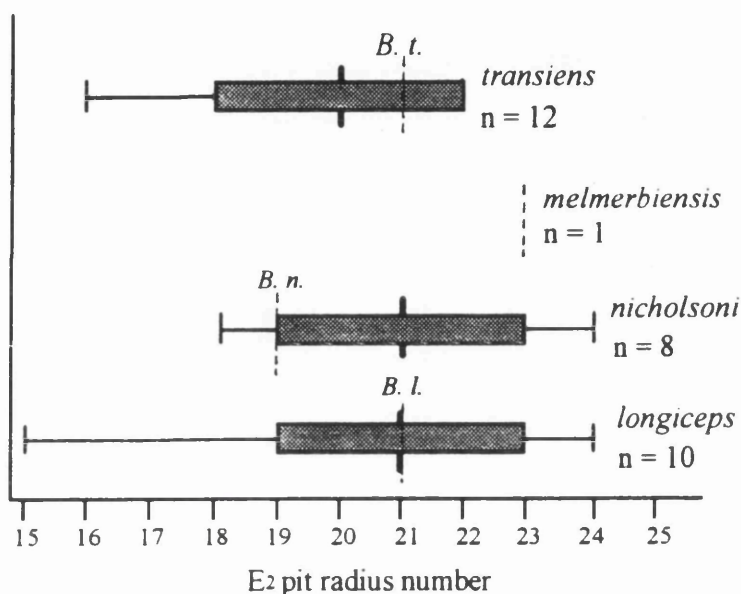
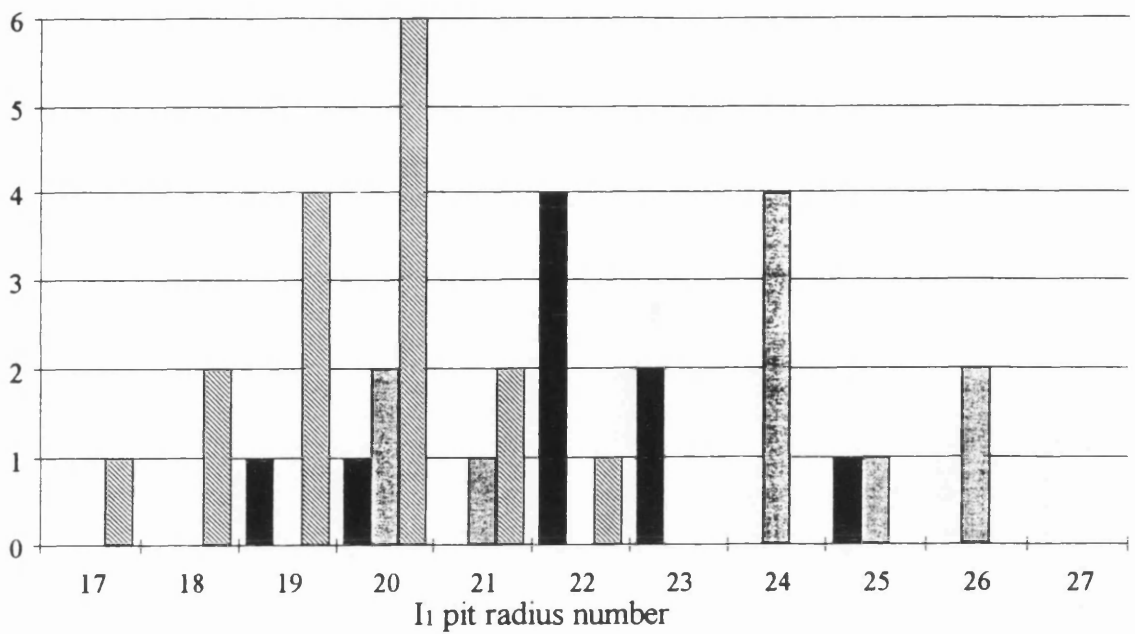
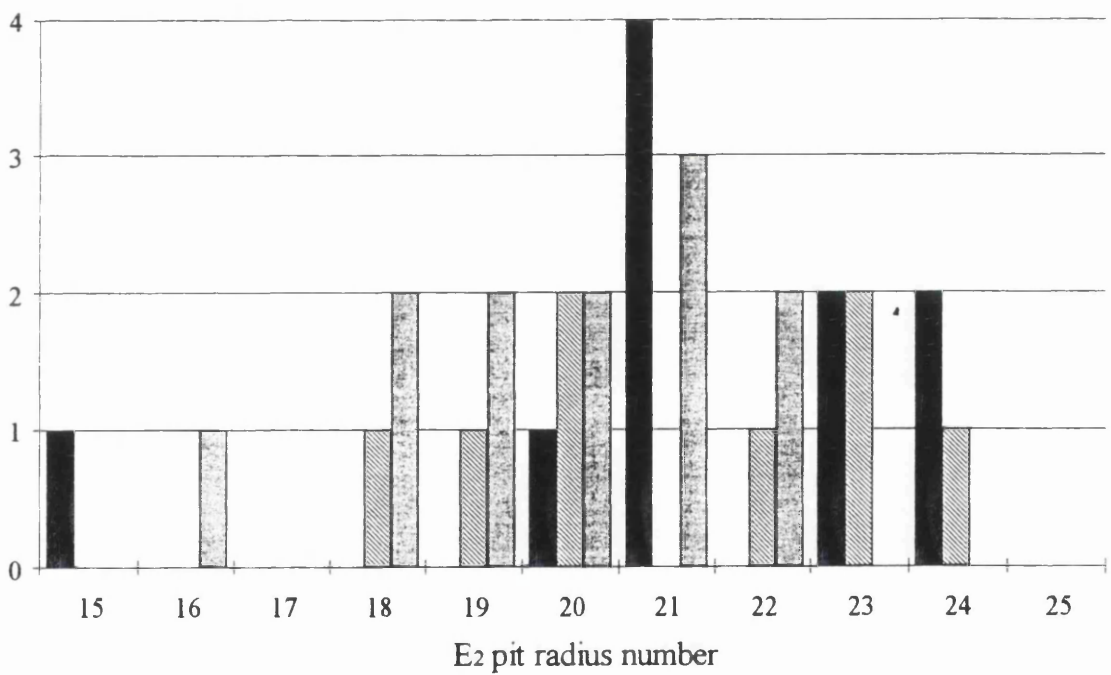


Fig. 5.8 (c) Range and mean charts for species as hitherto defined showing E2 pit radius number. The mean pit radius number is indicated by the thick vertical line, one standard deviation on each side of the mean is shown by the shaded rectangle and the range of variation is given by the horizontal line. If the sample contains the type locality of a species the type specimen is indicated by a vertical dashed line. Samples are from more than one locality.



■ *longiceps* n = 9
 ▨ *nicholsoni* n = 10
 ▩ *transiens* n = 16



■ *longiceps* n = 10
 ▨ *nicholsoni* n = 8
 ▩ *transiens* n = 12

Fig. 5.8 Frequency charts for species as hitherto defined showing (d) I_1 pit radius number and (e) E_2 pit radius number. Samples are from more than one locality.

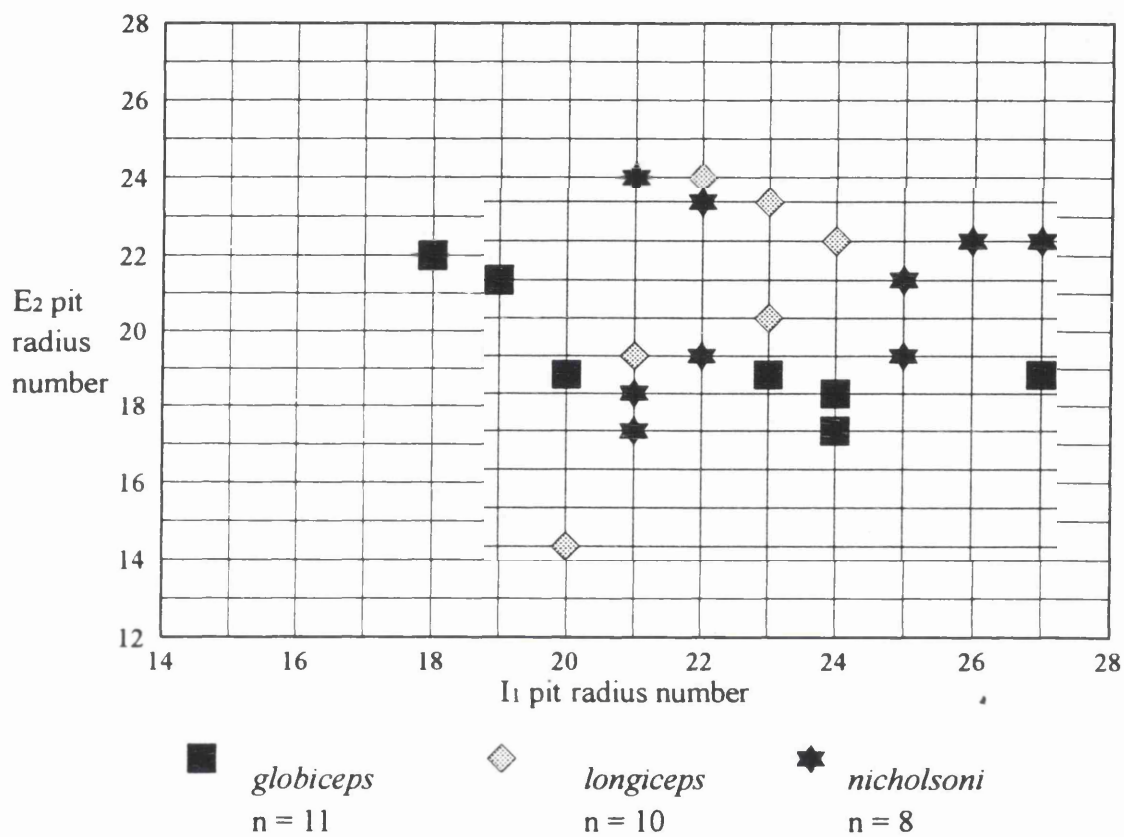


Fig. 5.8 (f) Chart showing I_1 pit radius number against E_2 pit radius number for the species as hitherto defined. Samples are from more than one locality.

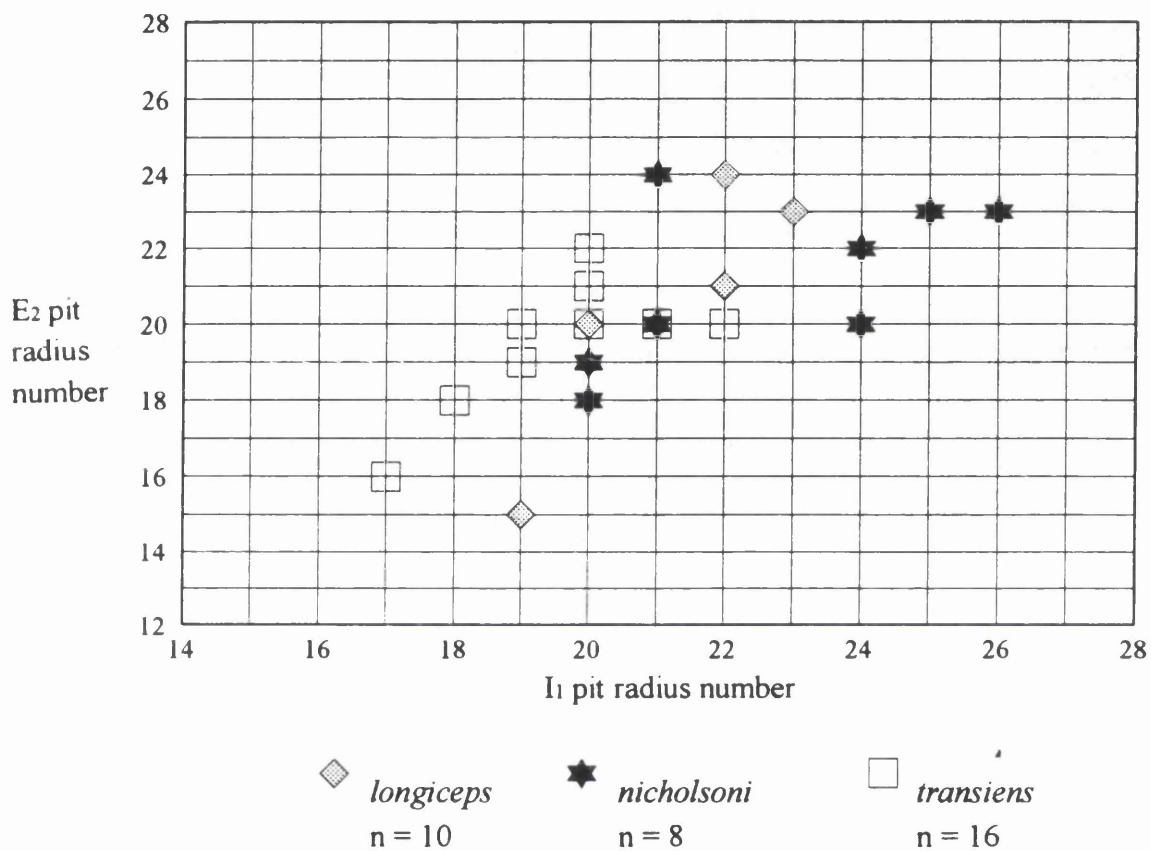


Fig. 5.8 (g) Chart showing I_1 pit radius number against E_1 pit radius number for the species as hitherto defined. Samples are from more than one locality.

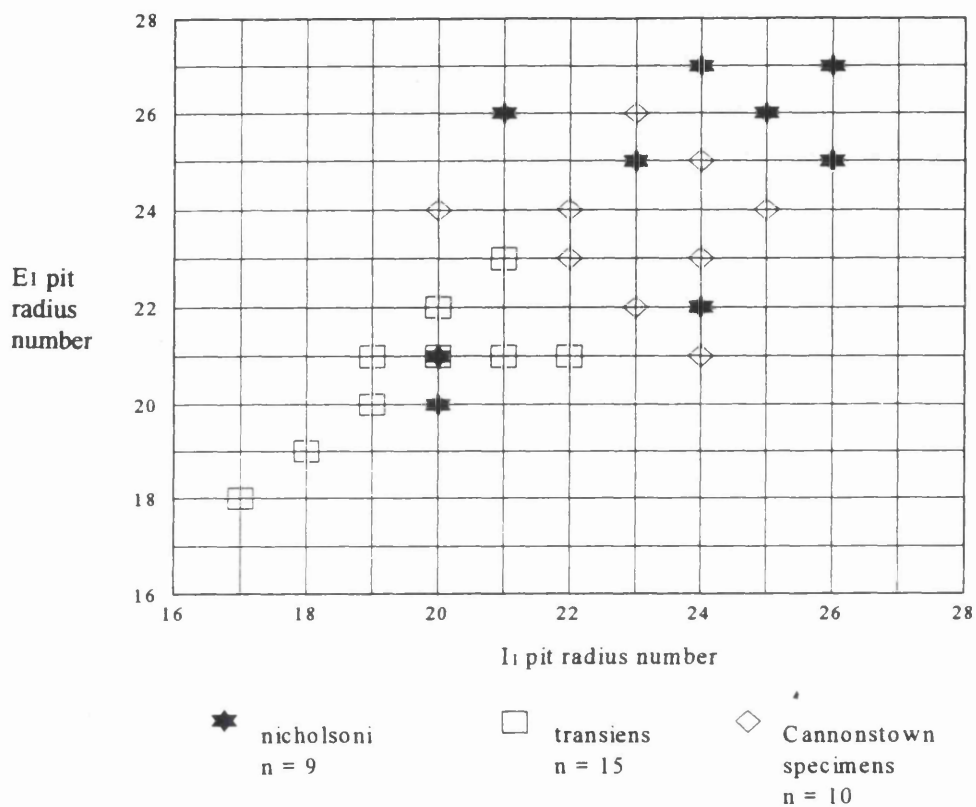


Fig. 5.8 (h) Chart showing I_1 pit radius number against E_1 pit radius number for the species as hitherto defined. Samples are from more than one locality.

5.6 Marshbrookian

The Marshbrookian saw the appearance of *B. transiens* (Bancroft, 1929) (type locality, the middle Marshbrookian *Dalmanella unguis* Biozone in the Cheney Longville Flags, which forms the upper half of a quarry in Marsh Wood, south of Marshbrook Station, Shropshire). This form has fringe characteristics similar to those of *nicholsoni* but a noticeably smaller pit count for all arcs (see Fig. 5.8) and *transiens* generally has radially sulcate E pits on the lower lamella anteriorly. The radial alignment of rows of pits continues further posteriorly than in *nicholsoni* due to I_n pits remaining a similar size to E_1 pits. The slight variation seen between *transiens* and the morphotypes which stratigraphically preceded it may only be a reflection of a steadily changing environment.

A particularly interesting specimen which was figured by Dean (1960) shows a damaged fringe which lead to premature termination of the E arcs. This could have been produced by loss of fringe tissue through tearing during moulting (see Plate 2, Fig. 10).

5.7 Actonian

Dean (1963) described rare specimens of *B. transiens* of Actonian age. A larger Hunterian sample was collected subsequently from a single bedding plane in the Acton Scott Formation one metre above the floor of Acton Scott Quarry, 460 metres west-north-west of St. Margaret's Church, Acton Scott, Shropshire. This sample is the youngest one known and marks the last record of the species and lineage of *Broeggerolithus*.

5.8 Irish and Scandinavian connections

A small sample of *Broeggerolithus* specimens of suspected Longvillian age (using associated brachiopod faunas) was collected by Dr. M. A. Parkes, from Cannonstown House, Kildare Inlier, County Kildare, Ireland (Parkes and Palmer, 1994). These specimens show similar fringe features to those of *nicholsoni*; they have a round cephalic outline, anteriorly all pits of are the same size and appear in sulcae on the upper lamella, E₂ pits generally are in radial alignment anteriorly with pits of other arcs. Statistically there is very little difference from *nicholsoni* (see Fig 5.8 (h)), whereas there is a larger difference between the Irish specimens and those of *transiens*. It seems likely that these Irish specimens represent a local population of *nicholsoni*.

Another location in eastern Ireland, Slieveroe, Rathdrum, Co. Wexford, has yielded specimens termed *B. cf. nicholsoni* by Brenchley *et al.* (1977). These specimens conform morphologically with *nicholsoni*, but the lack of full half-fringes has not allowed any statistical comparison. It is very probable that these are *nicholsoni* and therefore of Longvillian age.

Scandinavia has yielded possibly two *Broeggerolithus* species (Owen, 1983a) both of late Caradoc (approximately Woolstonian) age, *B. discors* (Angelin, 1854) (type locality in the Nakkholmen Formation at Koksabukten, Oslo) and *B. aff. discors* (of Owen, 1983a) from the "upper Chasmops beds", 300m south west of Tandsbyn station, Lockne, Jamtland, Sweden. The Norwegian *discors* differ from the Anglo-Welsh-Irish *Broeggerolithus* in that the E₂ pits are greatly reduced in size compared to the other arcs and E₂ also has a higher pit count (29.5 to 39 pits) leading to non-radial alignment with E₁. E₁ and I₁ pit counts for *discors* fall within the range of *nicholsoni* (22.5-26.5 cf. 20-27 and 22.5-27.5 cf. 20-26, respectively), though the F pit count is much less in *nicholsoni* (14-26 cf. 29-33). Some of the *discors* specimens also show a few (up to 7) E₃ pits in sulcae with E₂ pits. Rare specimens of *nicholsoni* are found with higher pit counts in the E₂ arc and these pits are smaller than is seen in the general population of *nicholsoni*, one particular specimen shows additional pits forming an E₃ arc (see Plate 2, Fig. 11). These features are common in *discors*, see Plate 2, Fig. 12. The Swedish aff. *discors* is thought to be the same age as *discors* but differs in lacking E₃ pits, E₂ pits appear larger and less irregular, E₁

has a lower E₁ pit count (22.5-25.5 cf. 25.5-29) and in having fewer F pits (20-27 cf. 29-33). It is possible that they are only geographical variants of *nicholsoni* with *discors* and the occasional *nicholsoni* (Pl. 2, Fig. 11) showing similar features to that of the ancestral form (e.g. small E₃ arc pit development) were redeveloped.

Summary

From the statistical and morphological analysis shown above it is clear that revision of several species should be made and this will be addressed in the next chapter.

In the early Harnagian a group of morphologically similar species (*harnagensis*, *caractaci paucus*, *praecursor* and *smeathenensis*) appeared in Wales and the Welsh Borderland, the only major difference being in the number of E arcs present. Depending on local conditions various morphotypes appeared together in differing degrees. As the Harnagian progressed only one form remained dominant, *caractaci caractaci* which appears very similar to *praecursor* but which contains a higher pit count for the E₃ arc and the occasional presence of an E₄ arc. This form survived well into the early Soudleyan perhaps on the verge of extinction before it disappeared.

With new relatively shallow water niches being opened up at the start of a marine regression the species *ulrichi* appeared in the latest Harnagian and is morphologically intermediate between the earlier *harnagensis* and the later *broeggeri*. This species differed from *harnagensis*, however, in its radial alignment of E₂ arc pits with those of the inner arcs. This new feature appears to be a standard character of pit distribution until the whole lineage died out in the Actonian.

The early Soudleyan saw the arrival of *broeggeri* with its variety of mesial pit distribution patterns. This gave way in the late Soudleyan to the morphologically similar *soudleyensis*, which was derived from a rare morphotype with *broeggeri* in the early Soudleyan. The Longvillian saw the arrival of two species and the loss of *soudleyensis*. Morphologically similar to *broeggeri*, *globiceps* is found only in southern South Shropshire, whilst a simpler fringed form, *nicholsoni*, is found co-

occurring with *globiceps* and in Northern England and Eastern Ireland. Much revision by previous authors has already been attempted for *nicholsoni* (see Chapter 6). In Shropshire the Alternata Limestone marks the base of the Woolstonian and contains *longiceps*, a species very similar to *nicholsoni* and restricted to Shropshire.

As the Marshbrookian Stage began *transiens* appeared in both Shropshire and Cross Fell, still showing radial pit alignment and similar to *nicholsoni* but with fewer pits in each arc. This species continued into the Actonian where it and the whole lineage died out.

Table 5.2 shows the main fringe characteristics and the present taxonomic names for all species in this study.

Range		Taxonomic name (as hitherto defined)	Radial alignment of E2 with inner arcs	E3 present	E4 present	E5 present
Harnagian	<i>B. harnagensis</i>	<i>Broeggerolithus transiens</i>	✓	x	x	x
	<i>S. c. paucus</i>	<i>Broeggerolithus longiceps</i>	✓	x	x	x
	<i>S. praecursor</i>	<i>Broeggerolithus nicholsoni</i>	✓	x	x	x
	<i>S. smeathenensis</i>	<i>Broeggerolithus globiceps</i>	✓	x	x	x
		<i>Broeggerolithus soudleyensis</i>	✓	x	x	x
		<i>Broeggerolithus breoggeri</i>	✓	x	x	x
		<i>Broeggerolithus ulrichi</i>	✓	x	x	x
		<i>Salterolithus caractaci caractaci</i>	x	✓	occ'nly anteriorly	x
		<i>Smeathenia smeathenensis</i>	x	✓	✓	✓
		<i>Salterolithus praecursor</i>	x	anterior to postero-lateral	x	x
		<i>Salterolithus caractaci paucus</i>	x	anteriorly	x	x
		<i>Broeggerolithus harnagensis</i>	occ'nly mesially	x	x	x
Soudleyensis						
Longvillian						
Woolstonian						
Marshbrookian						
Actonian						

Table 5.2. Cryptolithine species as hitherto defined from the Anglo-Welsh area and their approximate age ranges. This taxonomy is revised considerably herein (see Chapter 6).

PLATE ONE

Salterolithus harnagensis Bancroft

Morphotype D

[“*Salterolithus praecursor*”]

Lower Harnage Shale Formation, *Reuscholithus reuschi* Biozone. Coundmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 1. Cephalon, latex mould, BM.In52031, dorsal view, x2. Note E3 extending posteriorly.

Salterolithus harnagensis Bancroft

Morphotype B

[“*Salterolithus praecursor*”]

Lower Harnage Shale Formation, *Reuscholithus reuschi* Biozone. Coundmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 2. Cephalon, BM.In52041, dorsal view, x8. Note strong non-radial alignment of E2 pits.

Salterolithus harnagensis Bancroft

Morphotype B and Morphotype C

[“*Broeggerolithus harnagensis*” and “*Salterolithus praecursor*”]

Lower Harnage Shale Formation, *R. reuschi* Biozone. Swampy ground at back of Caer Caradoc, Approx. 0.33 km west of Robin's Tump, The Cwms, Church Stretton, Shropshire, England.

Fig. 3. Two cranidia, HM.A10436&7, dorsal view, x3. The two specimens show very different pit patterns outside of their E1 arcs.

Salterolithus harnagensis Bancroft, 1929

Morphotype A

["*Broeggerolithus harnagensis*"]

Lower Harnage Shale Formation, *Reuscholithus reuschi* Biozone. Coundmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 4. Partially complete trilobite, HM.A10868, dorsal view x4. Note pits appear similar in size and some radial alignment of pits anteriorly.

Salterolithus harnagensis Bancroft

Morphotype C

["*Salterolithus caractaci paucus*"]

Trilobite Dingle Shale Formation, loose material in stream section, Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales. (Probably from the upper reaches - Lower Trilobite Dingle Formation).

Fig. 5. Near complete trilobite, HM.A23145, dorsal view, x 3. Note E2 pits small, closely packed and out of alignment with inner arcs. E3 arc present mesially.

Lower Trilobite Dingle Shale Formation, upper reaches of stream section, Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales.

Fig. 10. Trilobite, N. Goodwin specimen, dorsal view, x1. Specimen shows a few E3 pits separated from E2 pits by thin walls.

Fig. 11. Cephalon, N. Goodwin specimen, dorsal view, x1. Note E3 present mesially. Some E3 pits are separated from E2 pits by thin walls.

Salterolithus harnagensis Bancroft
Morphotype C
[“*Salterolithus praecursor*”]

Lower Harnage Shale Formation, *Reuscholithus reuschi* Biozone. Countmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 8. Cranidium, HM.A10912, dorsal view, x 3. Note irregular pit distribution outside of E₁ arc.

Fig. 9. Lower lamella, HM.A10644, ventral view, x 2. Note some E₃ pits separated from E₂ pits by thin walls. E₂ showing some alignment with inner arcs.

Salterolithus carataci (Murchison)

Upper Harnage Shale Formation, *Salterolithus carataci* Biozone. Upper reaches of the stream section adjacent (south) of Wyrestche Quarry, Little Stretton, Shropshire, England.

Fig. 6. Lower lamella, HM.A10423/2a, ventral view, x3. Note E₃ extends towards genal angle. E₄ present mesially.

Salterolithus harnagensis Bancroft
Morphotype E
[“*Smeathenia smeathenensis*”]

Lower Harnage Shale Formation, *R. reuschi* Biozone. Wyrestche Quarry, behind the stable, near the southern end of Ragleth Hill, Little Stretton, Shropshire, England.

Fig. 7. Cranidium, HM.A10433/1, frontal view, x2. Specimen shows E₂ pits non-radially aligned with inner pits. Difference in pit sizes also clearly seen.

PLATE ONE

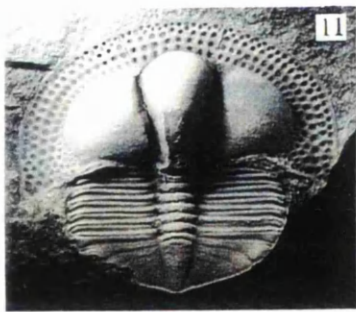


PLATE TWO

Broeggerolithus broeggeri ulrichi (Bancroft)
[“*Broeggerolithus ulrichi*”]

Upper Harnagian, Stream section in Middle House Dingle, Powys, Wales.

Fig. 1. Cranidium, latex cast, BM.In51897, dorsal view, x2. Note alignment of E2 pits. E1 arc appears higher than other arcs due to radial ridges.

Fig. 2. Cranidium, latex cast, BM.In51867, dorsal view, x2. Note alignment of E2 pits. E1 arc appears higher than other arcs due to radial ridges.

Upper Harnage Shale Formation, one kilometre south of Glenburrell, (Roundhouse), Shropshire, England.

Fig. 3. Cranidium, HM.A8901/1, dorsal view, x2. Strong radial alignment of all pits. Prominent radial ridges.

Broeggerolithus broeggeri broeggeri (Bancroft)
[“*Broeggerolithus broeggeri*”]

Lower Soudleyan, *B. broeggeri* Biozone. North east corner of Smeathen Wood, Onny River Valley, Cheney Longville, Church Stretton, Shropshire, England.

Fig. 4. Trilobite, latex mould, BM.In48937, dorsal view, x2. Note strong radial alignment of all pits. Outline of fringe curves in after most posterior E2 pit. Prominent radial ridges.

Fig. 6. Cephalon, BM.In50507, oblique antero-lateral view, x3. Rare specimen showing very limited E2 arc.

Lower Soudleyan, *B. broeggeri* Biozone, upper Chatwall Flags, band of decalcified sandy limestone from below the Chatwall Sandstone. Small Quarry exposure, below main quarry, The Pools, Chelmick Valley, Hope Bowdler, Church Stretton, Shropshire, England.

Fig. 8. Cranidium, BM.A18618/1, dorsal view, x2. Note strong radial alignment of all pits. Most common mesial pit pattern within *broeggeri* populations.

Broeggerolithus broeggeri broeggeri (Bancroft)
["*Broeggerolithus constrictus*"]

Basal Soudleyan. Millpond, SW of Caunant, Welshpool, Powys, Wales.

Fig. 5. Cephalon, latex mould, BM.In42101, dorsal view, x3. Note strong radial alignment of all pits. Outline of fringe curves in after most posterior E2 pit. Prominent radial ridges.

Broeggerolithus broeggeri globiceps (Bancroft)
["*Broeggerolithus globiceps*"]

Lower Longvillian, Middle Horderley Sandstone Formation. Quarry at top of west end of Rookery Wood, Horderley, Shropshire, England.

Fig. 7. Complete cranidium, BM.In49313, antero-lateral view, x2. Note strong radial alignment of all pits. Alignment of pits persists to genal angle. Prominent radial ridges.

Broeggerolithus nicholsoni (Reed)

Longvillian, Lower Melmerby Beds, Dufton Shale Formation, Cross Fell Inlier. Alston Road cutting, near Melmerby, Cumbria, England.

Fig. 9. Cranidium, SM.A29613, antero-lateral view, x3, lectotype. Shows radial sulcae mesially. Some loss of radial alignment of pits posteriorly.

Woolstonian, Dufton Shale Formation, Cross Fell Inlier. Harthwaite Sike, near Bow Hill in stream, near Brough-under-Stainmore, Cumbria, England.

Fig. 11. Latex cast of incomplete cephalon, BGS.PJ3702, dorsal view, x3. Note strong radial alignment of pits. Seven small pits visible at postero-lateral margin of fringe.

Broeggerolithus transiens (Bancroft)

Marshbrookian, Dufton Shale Formation, Cross Fell Inlier. Swindale Beck, near Knock, Cumbria, England.

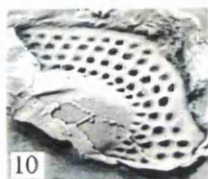
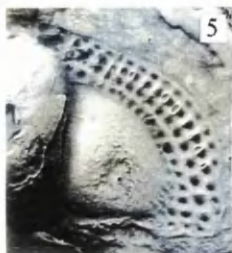
Fig. 10. Cephalon, latex mould, BM.In50222, dorsal view, x2. Specimen shows premature termination of E₁ and E₂ arcs, possibly due to injury.

Broeggerolithus discors (Angelin)

Nakholmen Formation. Nakholmen, Oslo.

Fig. 12. Internal mould of incomplete cranidium and pygidium, PMO H363, dorsal view, x2.1. Specimen shows small closely packed E₂ pits. (photograph courtesy of A. Owen).

PLATE TWO



6 Taxonomic and Evolutionary Resolution

From the results shown in the previous chapter it is clear that there are serious flaws in the present classification of the trilobites in this study which has led in the past to confusion and the tendency to over divide. They have in the past been classified, amongst other features, using the number of E arcs present and the number of pits therein. Depending on the quality of preservation it has often proved very difficult to distinguish the number and extent of these outer arcs, and with the overlapping ranges of some specimens and the coexistence in the same samples of different "species", classification has been somewhat ambiguous.

It is proposed in this chapter that a new, more workable classification, based on fringe pit patterns, morphology and statistics be used to reclassify these genera and species. The new system is based on the radial alignment patterns of the pits within the E arcs to distinguish genera and fringe morphology and pit counts to distinguish species. As is seen below one genus and many species names will be lost through synonymy but this will produce a more workable classification and enhanced stratigraphical use of these trilobites.

The arrangement of pits within the E₂ arc in relation to the radial rows produced from the pits in arcs I_n - E₁ clearly differentiates the early populations from nearly all later forms. In all Harnagian forms, except the latest form *ulrichi*, the E₂ arc pits are out of alignment with I_n - E₁ pits. All forms from *ulrichi* through to the last of the *Broeggerolithus* lineage, *transiens*, show E₂ pits in radial alignment with pits in the inner arcs. This alignment of the E₂ arc pits is of far greater significance at generic level than the number of E arcs and should be used as the primary criterion for the separation of *Broeggerolithus* and *Salterolithus*. It has been shown here that the number of E arcs, hitherto used to separate genera is unworkable. The type species of *Broeggerolithus* and *Salterolithus* satisfy the new criteria perfectly. By the same criteria, *Smeathenia* is synonymised with *Salterolithus* and its type species

Smeathenia smeathenensis becomes no more than an extreme morphotype of what becomes *Salterolithus harnagensis* - a binomen originally used by Bancroft (1929).

6.1 Non-radially Aligned Forms

It has been shown herein that pit distribution in the early Harnagian samples varies greatly in a single population, and it has commonly proved difficult to categorise some specimens which show irregular E arc pit distribution (see Section 5.1). The non-radial alignment of E₂ pits is seen both in species historically ascribed to *Salterolithus* and *Smeathenia* and in "*Broeggerolithus*" *harnagensis*. It is not present in post-Harnagian species, with the exception of *Salterolithus caractaci*. The type species of *Salterolithus*, *Trinucleus caractaci* Murchison, 1839 from the upper Harnagian shows this non-radial alignment. It is thus proposed that the early Harnagian forms previously termed *Broeggerolithus harnagensis* and *Smeathenia smeathenensis* are all synonymised within the genus *Salterolithus* as *S. harnagensis*.

Fringe morphology is very similar between all the morphotypes in the lower Harnagian, all have large well spaced pits in I_n, I₁ and E₁ arcs; all subsequent E arcs of pits are staggered (E₂ non-radially aligned) and a great variety of combinations of pit numbers can be seen from the E₂ arc outwards. This feature suggests interbreeding populations containing morphotypes of one species. These morphotypes of *Salterolithus harnagensis* are denoted as morphotypes (A) to (F), see Table 6.1. It is generally accepted that faunal abundance decreases with increasing water depth (e.g. Brenchley and Pickerill, 1993). The diversity of associated fauna is greater for populations of morphotypes A to D than it is for D to F and the later *S. caractaci* populations. Therefore, the presence and absence of different members of this population in particular environments suggests that the distribution of the morphotypes was probably related to local environmental conditions (see also Section 5.1). The morphotypes may reflect a species in the

process of separating into individual stocks (Hughes *et al*, 1975) in differing environments.

There is also a clear distinction between the early and late Harnagian forms which are assigned to the genus *Salterolithus*. Higher pit counts in all arcs particularly the E₂ arc of specimens historically assigned to *Salterolithus caractaci caractaci* distinguish them from the earlier lower pit count forms now assigned *S. harnagensis*. It is here proposed to reassign *S. caractaci caractaci* back to *S. caractaci*, losing its sub-species designation.

The classification of the Harnagian populations will be based on the dominant species within that particular population. This approach will allow for the variations in form, which would be expected in an interbreeding population in the early stages of separating. Within both the Harnagian populations a small number of specimens appear in which their pit counts vary markedly from the majority of the population. The early Harnagian contains high pit count specimens, similar to *caractaci*, and the late Harnagian *caractaci* populations contain some specimens with low pit counts. These may be early forms of *S. caractaci* and old morphotypes of *S. harnagensis* existing on the verge of extinction, or simply members of a very diverse population.

6.2 Radially Aligned Forms

In the late Harnagian, *ulrichi* appeared. Its fringe pit pattern relates it to the earlier *harnagensis* (now *S. harnagensis* morphotype A) but the E₂ pits are in radial alignment with E₁ to I_n pits. Under the new criteria it is now considered to be the oldest known *Broeggerolithus*. It also has generally low pit counts and some specimens show radial ridges and broad lists. These features link it to the next stratigraphically higher species *B. broeggeri*. It is considered here that there is insufficient morphological and statistical differences to keep *ulrichi* as a separate species and that it should be placed as a sub-species of *B. broeggeri*.

The type species of *Broeggerolithus* is *Cryptolithus broeggeri*, it is here assigned *Broeggerolithus broeggeri broeggeri*. Morphologically *B. b. broeggeri* is

very distinct from the earlier morphotypes, with its angular cephalic outline, caused by an increase in I₁ and E₁ pit sizes posteriorly, its distinct radial ridges and the radial alignment of the pits in the arcs I_n to E₂. Statistically it has fewer pits in each arc than *B. b. ulrichi* and has very narrow ranges of pit number variation in each arc. There are two distinct mesial pit patterns described in Section 5.3, the majority of specimens fall into the group which have continuous rows of pits or an extra E₁ pit mesially; the other group contains those specimens whose E₂ arc is absent mesially. The latter group is remarkably similar to *soudleyensis*, an upper Soudleyan form which can only be distinguished from *B. b. broeggeri* by the absence of E₂ pits mesially and posteriorly. It is therefore proposed that *soudleyensis* is a stratigraphical subspecies of *B. b. broeggeri*, with its origins in the early Soudleyan. *B. constrictus* is contemporary with *B. b. broeggeri* in the lower Soudleyan beds. It is morphologically very similar to *B. b. broeggeri*, except for the "constriction" of the fringe near the genal angle. It is proposed here that it is synonymous with *B. b. broeggeri*.

The form *globiceps* (Longvillian in age) is morphologically similar to *B. b. broeggeri*, though some *globiceps* specimens show a slight difference in glabella size and shape (see Section 5.4) and the variations between *globiceps* and *B. b. broeggeri* pit count statistics are very small. These slight differences may only be a reflection of the different environments in which the forms lived and it is proposed here that *globiceps* is synonymized with *B. b. broeggeri*.

B. nicholsoni is found in the Longvillian of N. England and SE. Ireland. It is morphologically different from the Soudleyan species and the contemporaneous *B. b. broeggeri* with the absence of radial ridges and differing pit sizes which posteriorly leads to some loss of pit alignment. Statistically it has relatively higher ranges and higher mean pit counts for all arcs than other species of *Broeggerolithus*, and should remain a valid taxon. *B. longiceps* is very similar morphologically and statistically to *nicholsoni*. However, some specimens of *longiceps* do show a slight difference in their glabella shape to those of *nicholsoni* (see Section 5.5) and this could be due to

their different environments. It is proposed here that *longiceps* is synonymous with *nicholsoni*.

The large *melmerbiensis* is possibly a rather old individual of *nicholsoni* and is here synonymized with the latter.

The species *transiens* remains a valid taxon having morphological and statistical differences from *nicholsoni* and shows radial alignment of pits posteriorly due to the pits of different arcs being of similar size. It is the last species of the genus *Broeggerolithus*.

The Norwegian *B. discors* is rather problematical as most specimens contain small non-radially aligned E₂ pits with the occasional presence of E₃ pits. Other specimens show E₂ pits of a more comparable size to the pits of I_n - E₁ arcs but still show some degree of non-radial alignment of E₂ pits. These features could suggest a tentative link to the genus *Salterolithus* rather than *Broeggerolithus*. However, the overall morphology is that of *Broeggerolithus* and the presence of small E₂ pits and occasional E₃ pits is seen in others of this genus, for example *nicholsoni* (see Pl. 2, Fig. 11). It has already been shown in Section 5.1 that specimens with high pit counts in their outer arcs appear to be better suited to deeper waters and the conditions in the Oslo region were becoming a more deep water offshore environment (Harper *et al.* 1984). The view here is that the loss of radial alignment is secondary and *discors* should remain within *Broeggerolithus*.

The Swedish *B. aff. discors* is morphologically and statistically similar to *nicholsoni* and is synonymized here with the latter.

Morpho- type	Radial alignment of E ₂ pits	Extent of E ₃	Extent of E ₄	Extent of E ₅	Previous taxonomic name
A	anteriorly only	x	x	x	<i>Broeggerolithus harnagensis</i>
B	x	x	x	x	<i>B. harnagensis</i>
C	x	anteriorly to postero- laterally (1-27 pits)	x	x	<i>Salterolithus caractaci paucus & S. praecursor</i>
D	x	complete (27-40 pits)	x	x	<i>S. praecursor</i>
E	x	complete (<27 pits)	anteriorly to postero- laterally (2-23 pits)	x	<i>Smeathenia smeathenensis</i>
F		complete (>27 pits)	complete (2-36 pits)	anteriorly	<i>S. smeathenensis</i>

Table 6.1. The various morphotypes of Salterolithus harnagensis present in the lower Harnagian with their previous taxonomic names, their new morphotype category letters and the main fringe features used to distinguish them. x = absent.

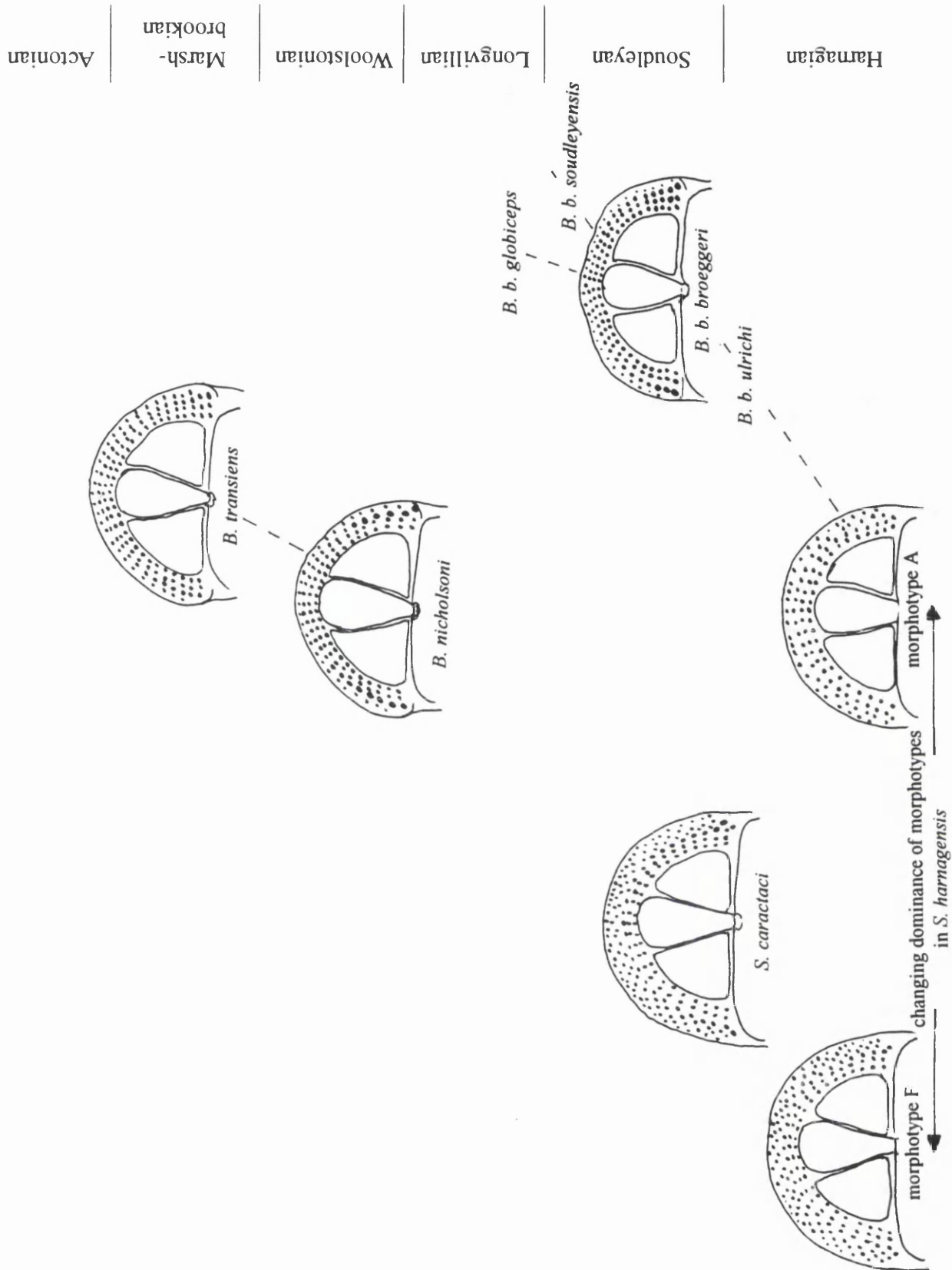


Fig. 6.1. Diagram of the summary of the new classification. The diagram shows the stratigraphical positions and supposed relative water depths preferred by the species, subspecies and morphotypes of the two recognised genera.

7 Taxonomy

Family TRINUCLEIDAE, Hawle & Corda, 1847

Diagnosis. Trilobites in this family are characterised by their bilamellar cephalic fringe possessing numerous opposed pits on external surfaces. The dorsal inframarginal suture, becoming dorsal along posterior margin of the fringe. The genal spines are on the lower lamella. The thorax consists of six segments, with distal extremities of pleurae deflected downwards. The pygidium is triangular in outline and the posterior and lateral margins are deflected nearly vertically downwards. Pygidial and thoracic doublure are very narrow.

Subfamily CRYPTOLITHINAE Angelin, 1854

Diagnosis. Fringe with E, I and F pits well developed. I_n not cut-off by outer I arcs. Glabella high, clavate, non-carinate with small basal lateral glabellar furrows and two further faint pairs. Occipital spine present.

Type genus. *Cryptolithus* Green, 1832

Discussion. There are two distinct types of stock within the cryptolithines. The Anglo-Welsh stock contains a fixed number of I arcs and a varied number of E arcs. The other stock is from North America and contains the genera *Cryptolithus* Green, 1832 and *Cryptolithoides* Whittington, 1941, these possess numerous I arcs and only one E arc. Both the Anglo-Welsh and the North American cryptolithines may have their ancestral roots within the Chinese *Yinpanolithus* Lu, 1974 (see Chapter 8).

Genus *SALTEROLITHUS* Bancroft, 1929

Diagnosis. Rounded cephalic outline. Arcs I_n , I_1 and E_1 complete and their pits are in radial alignment. Arc E_2 is complete and shows no radial alignment with the inner pits. Arcs outside E_2 are present to varying degrees. Girder distinct and first internal pseudo-girder weakly developed.

Type-species. *Trimucleus caractaci* Murchison, 1839 from the Harnagian of Welshpool, Powys, Wales.

Other forms included;

Salterolithus harnagensis Bancroft, 1929

Distribution. Caradoc of Wales and the Welsh Borderland (Harnagian to lower Soudleyan).

Discussion. The distinction between *Salterolithus* and *Broeggerolithus* has hitherto been based purely on E arc numbers, a criteria shown to be unworkable. The only workable and useful criterion to separate these two genera is the radial alignment of pits in the outer E arcs with those in arcs I_n to E_1 . All forms showing non-radial alignment of E_2 pits with pits in arcs I_n to E_1 are here synonymised with *Salterolithus*. This includes some taxa which in recent decades have been considered to belong in *Broeggerolithus*. Moreover, considerable reassessment of existing species is necessary to take into account the variation in the evolving populations of this genus. The original concept of type-species *S. caractaci* remains unaltered, *S. harnagensis* is revised and contains *Broeggerolithus harnagensis*, *S. praecursor* and *S. caractaci paucus* and *Smeathenia smeathenensis*, the type species of *Smeathenia* Dean. Morphotypes have been erected within the species *S. harnagensis* to accommodate the wide range of fringe pit distribution patterns seen in its synonymised species.

Salterolithus caractaci (Murchison)

Plate 1, Fig. 3, Pl. 3, Figs. 1-5, Text Figs. 5.3, 5.1, 6.1.

1839. *Trinucleus caractaci* Murchison, p. 659, pl. 23, figs. 1a, b, c.

1960. *Salterolithus caractaci* (Murchison); Dean, p. 96, 98, pl. 15, figs. 1, 2, 4, 6, 9.

1963. *Salterolithus caractaci* (Murchison); Dean, p. 11.

1968. *Salterolithus caractaci* (Murchison); Greig *et al.*, p. 109.

1975. *Trinucleus caractaci* Murchison; Hughes, p. 581, pl. 10, figs. 119.

1995. *Salterolithus caractaci* (Murchison); Pratt, p. 48.

For full synonymy list see Dean, 1960, p.97.

Diagnosis. E₂-E₄ arc pits non-radially aligned and smaller than inner arcs. Arcs E₂ and E₃ complete, E₄ present mesially in a few specimens. High pit counts in all arcs. Recorded range and mean of pit counts for I_n = 22-29 (25); I₁ = 25-28 (26); E₁ = 26-30 (28); E₂ = 26-34 (30); E₃ = 10-40 (25); E₄ = 12; E₂ termination = n to n-3 (n-2); E₃ termination = n-2 to n-8 (n-5); F pits = 27-33 (29).

Lectotype. An incomplete cranidium with a complete left-hand side fringe. Selected by Cave (1957, p. 284); BGS Geol. Soc. coll. 6829; original of Murchison 1839, pl. 23, fig. 1b, probably Harnagian in age from Trilobite Dingle, Welshpool, Powys, Wales.

Distribution. Material assigned to the late Harnagian and Soudleyan in Wales, Shropshire and the Shelve Inlier.

Description. For a full description see Cave (1957). Cephalon rounded in outline. Arcs I_n to E₁ are complete and in good radial alignment, pits increase in size gradually towards the posterior of the fringe. Pits of arcs E₂ and outwards are all smaller than those of the inner arcs. Pits in the E₂ arc are positioned between the radial rows of the inner arcs, E₃ arc pits are usually in radial alignment with I_n to E₁

pits, if E₄ pits are present they align with E₂ pits. Broad concentric bands are present between arcs I_n-I₁ and I₁-E₁, some specimens show a narrow band between E₁-E₂.

Discussion. The lectotype was chosen by Cave (1957 : 284) from one of Murchison's syntypes. This specimen did not possess a locality label and concern had been expressed by Whittington (1958: 83) that this specimen was from Wistanstow, as mentioned in the register and not from Trilobite Dingle as Cave, on lithological grounds, believed. Dean (1960 : 97) agreed with Cave and suggested that a mistake had been made in the original registration of the specimen.

The species *S. caractaci* is also found along with specimens of *Broeggerolithus broeggeri broeggeri* in beds of lower Soudleyan age. They can be easily distinguished by the extra E arcs in *S. caractaci* (see Figs. 5.3, 5.4, 5.5) and *B. b. broeggeri*'s prominent radial ridges. Specimens of *S. caractaci* show generally significant higher pit counts than *S. harnagensis*, for example; E₁ arc range 26-30 mean (28) cf. 20-25 (23), E₂ arc 26-34 (30) cf. 22-30 (25), E₃ arc 10-40 (25) cf. 2-37 (16). The most significant difference is seen when the sum of the arcs outside E₁ is compared *S. caractaci* 52-79 (64) cf. *S. harnagensis* 27-89 (47). The range of the latter is pushed higher as it contains a few specimens which possess four or more E arcs, the presence of these previously termed *Smeathenia* specimens produce higher end members of the pit count ranges than the majority of the population would show.

Salterolithus harnagensis Bancroft

Plate 1, Figs 2-5,7-11, Pl. 3, Figs. 6-15, Pl. 4, Figs. 1-8, Text-Figs. 5.3, 6.1,

Table 6.1

1929. *Salterolithus harnagensis* Bancroft, p. 79, pl. 1, figs. 1, 2.
1929. *Salterolithus harnagensis* var. Bancroft, p. 80.
1929. *Salterolithus* sp. Bancroft, p. 81.
1929. *Salterolithus* cf. *intermedius* Bancroft, p. 82.
1933. *Salterolithus harnagensis* Bancroft, table 3.
1949. *Salterolithus* aff. *harnagensis* Bancroft, p. 291, pl. 10, fig. 15.
1955. *Salterolithus* cf. *harnagensis* Bancroft; Whittington and Williams,
p. 420-421, pl. 10, figs. 94-96, 100, 101, text-fig. 6.
1956. *Salterolithus harnagensis* Bancroft; Harper, p. 386.
1958. "*Salterolithus*" *harnagensis* Bancroft; Whittard, p. 83.
1958. *Salterolithus harnagensis* Bancroft; Dean, p. 200-201.
1958. *Salterolithus smeathenensis* Bancroft; Dean, p. 201, pl. 26, fig. 4.
1958. *Salterolithus caractaci* (Murchison); Dean, p. 201-202. pl. 26, fig. 5.
1960. *Broeggerolithus harnagensis* (Bancroft); Dean, p. 103, 105-107,
pl. 16, figs. 5, 9, 13.
1960. *Broeggerolithus* cf. *harnagensis* (Bancroft); Dean, p. 107-108, pl. 16,
figs. 7, 11.
1960. *Broeggerolithus* sp. Dean; p. 108-109, pl. 16, fig. 2.
1960. *Smeathenia smeathenensis* (Bancroft); Dean p. 100-102, pl. 13, figs. 7,
10-16.
1960. *Salterolithus praecursor* (Dean); p. 98-100, pl. 15, figs. 3, 5, 7, 8,
10-12.
1963. *Broeggerolithus harnagensis* (Bancroft); Dean, p. 10.
1963. *Salterolithus praecursor* Dean; p. 10.

1975. *Broeggerolithus harnagensis* (Bancroft); Hughes *et al.*, p. 580.
1975. *Salterolithus praecursor* (Dean); Hughes *et al.*, p. 580-581, pl. 10, fig. 117.
1975. *Salterolithus* sp. Hughes *et al.*, pl. 10, fig. 118.
1975. *Salterolithus caractaci paucus* Cave; Hughes *et al.*, p. 581.
1975. *Smeathenia smeathenensis* (Bancroft); Hughes *et al.*, p. 581.
1983. *Salterolithus caractaci paucus* Cave; Owen, p. 242, pl. 34, fig. 6.

Diagnosis. Cephalic outline is rounded and fringe morphology is simple. Arcs E₃ - E₅ present to varying degrees. Recorded range and mean of pit counts for I_n = 11-28 (22); I₁ = 19-27 (23); E₁ = 19-30 (24); E₂ = 17-34 (26); E₃ = 1-40 (18); E₄ 2-36 (16); E₂ termination = n to n-5 (n-2); E₃ termination = n-1 to n-10 (n-5); F pits = 11-31 (23).

Lectotype. Complete cranidium. Selected by Dean (1960, p. 107): BM In42081, from the Smeathen Wood Formation (Harnagian) of the south bank of Coundmoor Brook, south-west of Harnage Farm, near Evenwood, Shropshire, England.

Distribution. Material assigned to the Derfel Limestone, lower Trilobite Dingle Shale Formation, Smeathen Wood Formation and lower Harnage Shale Formation of Early Harnagian age in Wales and South Shropshire.

Description. Cephalic outline is well rounded. Glabella moderately convex and slightly clavate anteriorly. Genal lobes smooth, gently convex and separated from the glabella by straight axial furrows each with a small hypostomal pit situated near the fringe. Occipital ring distinct and the occipital furrow is faint. The remains of an occipital spine is present in some specimens. The posterior margin is slightly convexed towards the genal spines. Cephalic fringe is broad. Radial ridges are absent. Pits in arcs I_n-E₁ show good radial alignment and are larger than those in the outer arcs. Broad concentric bands are seen between I_n and I₁ and I₁ and E₁. Arc E₂ is present and complete with its pits positioned between the radial rows of the

inner arcs. Arc E₃, E₄ and E₅ may be present as either a few pits anteriorly or complete. The different morphotypes are described in the table below.

Discussion. Specimens of this species appear to be associated with certain depths of water. Forms containing incomplete E₃ arcs and low pit counts are found in association with high faunal diversity indicating shallower waters. Populations dominated by complete E₃ arcs and high pit counts appear with lower faunal diversities. Morphotypes are selected using their fringe morphology see Sections 5.1, 6.1, Figs. 5.1, 5.3, 5.4, 6.1, Table 5.2 and 6.1. Morphotypes (A) and (B) contain only four arcs, no E₃ arc and are the previously termed *Salterolithus harnagensis* forms. Morphotype (A) shows some radial alignment of pits in all arcs anteriorly, this feature does not extend past the line of the axial furrow (Plate 3, Figs. 6-8). Morphotype (B) shows no radial alignment of pits in the E₂ arc with the other arcs (Plate 3, Figs. 9, 10). All the forms previously termed *Salterolithus caractaci paucus* are contained within morphotype (C) along with forms of *Salterolithus praecursor* which show the E₃ arc extending no further than the anterolateral position, E₃ arc generally contains 1-27 pits (Plate 3, Figs 11-15 and Pl. 4, Figs. 1-2). Morphotype (D) contains all other forms previously known as *Salterolithus praecursor*, these show arc E₃ extending laterally to near the genal angle, E₃ containing up to 40 closely packed pits (Plate 4 Figs. 3-5). Morphotype (E) contains those forms previously known as *Smeathenia smeathenensis* which show a complete E₃ arc (up to 39 pits) and an E₄ arc extending to the posterolateral position. The final morphotype (F) contains specimens of *Smeathenia smeathenensis* which have a complete E₄ arc (up to 36 pits) and some forms which may show pits in an E₅ arc (Plate 4, Figs. 6-8). The irregularity of E₄ pits can make identifying another outer arc very difficult.

Genus BROEGGEROLITHUS Lamont, 1935

Diagnosis: Arcs I_n , I_1 , E_1 and E_2 present and complete. Pits in rows I_n to E_2 show radial alignment generally over entire fringe. Girder distinct and first internal pseudo-girder weakly developed.

Type-species. *Cryptolithus broeggeri* Bancroft, 1929 from the Caradoc Series of Shropshire, England. [= *B. broeggeri broeggeri*]

Other included forms:

B. broeggeri ulrichi (Bancroft, 1949)

B. broeggeri soudleyensis (Bancroft, 1929).

B. broeggeri globiceps (Bancroft, 1929).

B. nicholsoni (Reed, 1910).

B. transiens (Bancroft, 1929).

B. discors (Angelin, 1854).

Distribution. Caradoc of Wales and the Welsh Borderland (latest Harnagian to Actonian), Northern England (Longvillian to Marshbrookian), Eastern Ireland and Belgium (Longvillian) and Scandinavia (approximately Woolstonian).

Discussion. With the reassessment of species herein, the genus *Broeggerolithus* now only includes those species which show good radial pit alignment for all arcs, with the exception of *discors* which shows some non-radial alignment of E_2 pits (see Section 6.2 and later). This has resulted in the reassignment of *harnagensis* to the genus *Salterolithus* and considerable reclassification of the early forms of *Broeggerolithus*. There are now four species of *Broeggerolithus* recognised here: the oldest *B. broeggeri* containing the subspecies *B. broeggeri ulrichi*, *B. broeggeri broeggeri*, *B. broeggeri soudleyensis* and *B. broeggeri globiceps*; *B. nicholsoni* within which *B. longiceps* and *B. melmerbiensis* are here

synonymised together with the Irish, Belgium and one of the Scandinavian forms; the problematical *B. discors* from Norway; and *B. transiens* morphologically the simplest of all the *Broeggerolithus* forms and last of the lineage. Emended diagnoses for all of the species are given below together with synonymies and discussions.

Broeggerolithus broeggeri (Bancroft)

Diagnosis. Cephalon appears angular in outline. I_n - E_1 present and complete. E_2 generally incomplete mesially, pit size decreases posteriorly and the arc terminates well in front of the posterior E_1 pit. E_2 pits in radial alignment with pits of arcs I_n - E_1 and rows generally flexed towards the genal angle. Prominent radial ridges seen laterally between I_1 and E_2 .

Discussion. *Broeggerolithus broeggeri* now contains four chronological subspecies. These show enough variation in features for their individual identification but all contain the general characteristics, good radial rows and prominent radial ridges, of the type species.

Broeggerolithus broeggeri broeggeri (Bancroft)

Plate 2, Figs. 3-5,7, Plate 4, Figs. 9-12, Text-Figs. 5.5, 5.6, 5.7, 6.1.

1929. *Cryptolithus broeggeri* Bancroft, p. 85, pl. 1, figs. 6-8.

1933. *Broeggeria broeggeri* (Bancroft); Bancroft, p. 2, tables 2, 3.

1935. *Broeggerolithus broeggeri* (Bancroft); Bancroft, p. 333.

1938. *Cryptolithus broeggeri* Bancroft; Whittington, p. 425, 428, 436, 450.

1940. *Broeggerolithus broeggeri* (Bancroft); Whittington, p. 245.

1941. *Broeggerolithus broeggeri* (Bancroft); Whittington, p. 24.

1949. *Broeggerolithus broeggeri* (Bancroft); Bancroft, p. 298, pl. 9, figs. 4, 5.
1958. *Broeggerolithus broeggeri* (Bancroft); Whittard, p. 89, pl. 12, figs. 7 - 13.
1958. *Broeggerolithus broeggeri* (Bancroft); Dean, p. 203, pl. 26, fig. 7.
1960. *Broeggerolithus broeggeri* (Bancroft); Dean, pp. 111 - 112, pl. 16, figs. 3, 10.
1960. *Broeggerolithus* cf. *broeggeri* (Bancroft); Dean, pp. 112-113, pl. 16, figs. 4, 8, 14.
1960. *Broeggerolithus constrictus* Bancroft; Dean, pp. 113-114, pl. 16, figs. 6, 12.
1963. *Broeggerolithus broeggeri* (Bancroft); Dean, pp. 11-15.
1966. *Broeggerolithus broeggeri* (Bancroft); Whittington, p. 85, pl. 12, figs. 4, 6-8, 10.
1968. *Broeggerolithus broeggeri* (Bancroft); Greig *et al.*, p. 109.
1975. *Broeggerolithus broeggeri* (Bancroft); Hughes *et al.*, p. 580, pl. 10, figs. 115, 116.
1975. *Broeggerolithus* cf. *broeggeri* (Bancroft); Hughes *et al.*, p. 580.
1975. *Broeggerolithus constrictus* (Bancroft); Hughes *et al.*, p. 580.
1995. *Broeggerolithus broeggeri* (Bancroft); Pratt *et al.*, p. 48, pl. 9, figs. f, g.

Diagnosis. Angular cephalic outline. Four arcs present. Anteriorly radial rows flexed towards the genal angle and posteriorly they are flexed away from the genal angle. Pits in arcs I_1 and E_1 increase in size posteriorly. E_2 arc terminates well in front of the posterior E_1 pit. Prominent radial ridges between I_1 and E_2 . Recorded I_n pit counts between 17-24 mean(20); I_1 = 20-23 (21); E_1 = 20-24 (21.5); E_2 = 18-22 (20); E_2 termination = n to n-5 (n-2); F pits = 11-26 (18).

Lectotype. Well preserved cranium. Selected by Whittard (1958, p. 89); BM In42077, from the Glenburrell Formation (Soudleyan) of Smeathen Wood, Horderley, Shropshire, England.

Distribution. Early to middle Soudleyan of Wales, Shelve Inlier and south Shropshire.

Description. Cephalic outline angular anterolaterally. Glabella moderately convex and slightly clavate. Genal lobes smooth, gently convex and separated from the glabella by broad, moderately deep axial furrows each with a small hypostomal pit situated near to the fringe. Occipital ring distinct and the occipital furrow is faint. The remains of an occipital spine is present in some specimens. Posterior margin appears sinuous and inclined towards the front. Cephalic fringe narrowest anteriorly. Well pronounced radial ridges between pits of E_1 arc, extend to the arc either side of E_1 arc so giving the impression that the E_1 arc is raised higher than the other arcs. Pits of all arcs are approximately the same size anteriorly, those in arcs I_1 and E_1 become increasing large posteriorly where the E_2 pits decrease slightly giving the impression they are being pinched out. Mesially there are a number of different pit arrangements, the most common pattern has two complete radial rows of pits either side of the median line and one isolated E_1 pit on the median line (see Fig. 5.6 for more details).

Discussion. In the past a great deal of importance has been placed on the arrangement of the mesial pits, particularly those of E_2 , but it has been shown herein that each *B. b. broeggeri* population contains a wide variation of mesial pit patterns (see Fig. 5.6 and Plate 4, Figs. 9, 10). Therefore, this feature must be used in conjunction with other morphological and fringe pit statistical features to classify specimens. *B. constrictus* Dean is synonymised here within *B. b. broeggeri* as there are insufficient differences morphologically and statistically between it and *B. b. broeggeri*, except for the premature termination of the outer arcs near the genal angle, usually E_2 (see Section 5.3 and Plate 4, Figs 11, 12). This may be caused by the loss of tissue by tearing free from the fringe lamellae which had not separated

correctly during moulting. This type of injury is also found in other species of trinucleids (e.g. Owen, 1983, 1985). However, as this feature occurs most frequently in a small population in Middle House Dingle, this could be a local genetic effect.

A single specimen from the population of *B. b. broeggeri* in the Hagley Shales of the Shelve Inlier was classified as *Broeggerolithus* sp. (Whittard, 1958, p. 91-92, pl. 12, fig. 15) shows closely packed E₂ pits and no radial ridges. It is difficult to establish the importance of the specimen though its features are very similar to the stratigraphically younger specimen previously designated *B. melmerbiensis* and other closely allied forms now synonymised with *B. nicholsoni*.

Broeggerolithus broeggeri ulrichi (Bancroft)

Plate 2, Figs. 1,2, Plate 4, Figs. 13, 14, Text-Figs. 5.5, 6.1.

1933. *Ulricholithus ulrichi* Bancroft, p. 2, table 2.

1949. *Salterolithus (Ulricholithus) ulrichi* (Bancroft); Bancroft, p. 296, pl. 9, fig. 14.

1955. *Salterolithus* cf. *harnagensis* Bancroft; Whittington and Williams, p. 420, pl. 40, figs. 94-96, 100, 101.

1958. *Salterolithus (Ulricholithus) ulrichi* (Bancroft); Whittard, p. 84, pl. 12, fig. 1.

1958. *Ulricholithus ulrichi* Bancroft; Dean, pp. 200 - 202, pl. 26, fig. 6.

1960. *Broeggerolithus ulrichi* (Bancroft); Dean, pp. 109-111, pl. 17, fig. 10, 11.

1963. *Broeggerolithus ulrichi* (Bancroft); Dean, pp. 11, 15.

1966. *Broeggerolithus* cf. *ulrichi* (Bancroft); Whittington, pp. 84-85, pl. 12, figs. 1-3,5.

1975. *Broeggerolithus ulrichi* (Bancroft); Hughes *et al.*, p. 580.

1975. *Broeggerolithus* cf. *ulrichi* (Bancroft); Hughes *et al.*, p. 580.

Diagnosis. Arcs I_n - E_2 complete. Radial ridges may be present. Recorded range and mean of pit counts: I_n = 18-23 (21.5); I_1 = 19-23, mean (21); E_1 = 20-24 (22.5); E_2 = 17-27 (22.5); E_2 termination = n-1 to n-5 (n-4); F pits = 24-30 (27).

Holotype. An incomplete upper lamella cephalon showing a complete left hand fringe. Selected by Dean (1960, p. 111); BM In42371, from the Glenburrell Formation (Harnagian) of the Middle House Dingle, near Middle House, 5.5 km. north of Welshpool. Powys, Wales.

Distribution. Wales and South Shropshire in material from latest Harnagian and Early Soudleyan age.

Description. Cephalic outline angular. All four arcs complete, I_n - E_1 arc pits increase in size posteriorly. E_2 arc pits may become smaller posteriorly giving impression of being pinched out. Radial ridges may be present between E_1 arc pits giving the impression of that being raised higher than neighbouring arcs.

Discussion. Statistically *B. b. ulrichi* has similar pit counts to *B. b. broeggeri*, (see Fig. 5.5) e.g., I_1 = 20-23 (21) cf. 20-23 (21) and E_1 = 20-24 (22.5) cf. 20-24 (21.5), except for the outer most arc E_2 = 17-27 (22.5) cf. 18-22 (20). This higher pit count in the E_2 arc and the higher termination number n-1 to n-5 (n-4) cf. n to n-5 (n-2) produces an outer arc of smaller and more closely packed pits than is seen in *B. b. broeggeri*. The Welsh populations show generally higher pit counts than the Shropshire populations, possibly due deeper water conditions in Wales (see earlier). Morphologically the outline of the cephalon is less angular, the increase in pit size posteriorly and the development of radial ridges are far less extreme than in *B. b. broeggeri* (Plate 4, Figs. 13, 14).

Broeggerolithus broeggeri soudleyensis (Bancroft)

Plate 2, Fig. 6, Pl. 4, Figs. 15,16, Text-Figs. 5.7, 6.1.

1929. *Cryptolithus soudleyensis* Bancroft, p. 86, pl. 1, figs. 9-11.
1933. *Broeggeria soudleyensis* (Bancroft); Bancroft, table 2.
1935. *Broeggerolithus soudleyensis* (Bancroft); Bancroft, p. 334.
1938. *Cryptolithus soudleyensis* Bancroft; Whittington, p. 451.
1940. *Broeggerolithus soudleyensis* (Bancroft); Whittington, p. 245.
1941. *Broeggerolithus soudleyensis* (Bancroft); Whittington, p. 27.
1945. *Broeggerolithus soudleyensis* (Bancroft); Bancroft, pp. 210-211, 239.
1958. *Broeggerolithus soudleyensis* (Bancroft); Whittard, p. 91, pl.12, fig.14.
1958. *Broeggerolithus soudleyensis* (Bancroft); Dean, p. 204, pl.26, fig.8.
1960. *Broeggerolithus soudleyensis* (Bancroft); Dean, pp. 115-117, pl.17,
fig.1,5-9, 17.
1963. *Broeggerolithus soudleyensis* (Bancroft); Dean, p. 11,15.
1968. *Broeggerolithus soudleyensis* (Bancroft); Greig *et al.*, p. 110.
1975. *Broeggerolithus soudleyensis* (Bancroft); Hughes *et al.*, p. 580.

Diagnosis. Arcs I_n , I_1 and E_1 complete, E_2 arc pits absent mesially and posteriorly. Radial ridges well developed. Recorded pit count ranges and means for I_n = 16-22 (19); I_1 = 17-22 (19); E_1 = 19-23 (21); E_2 = 11-18 (15); E_2 termination = n-2 to n-4 (n-3); F pits = 15-20 (18).

Lectotype. A poorly preserved cranium with no complete half fringe. Selected by Morris; BM In49025, from the Soudleyan of Soudley Quarry, Ticklerton, Shropshire, England.

Distribution. This species is most common in the late Soudleyan of Shropshire and is used as the zonal index there. It is found in the Soudleyan of the Shelve Inlier and it is also present in the Soudleyan - early Longvillian of Wales.

Description. Essentially the same morphology as *B. b. broeggeri* but a significant number of E₂ arc pits (generally between 3 and 6) are absent mesially or mesially and posteriorly.

Discussion. Except for the lower pit counts of all arcs, especially E₂ 11-18 (15) cf. 18-22 (20) there is very little difference between *B. b. broeggeri* and *B. b. soudleyensis*. Morphologically they are very similar and statistically the ranges and mean pit counts differ only slightly possibly reflecting adaptations to the continuing marine regression in the area. As described in Section 5.3, there are specimens in the *B. b. broeggeri* populations which appear to be similar in form to *B. b. soudleyensis*, these rare forms were probably the forms which gave rise to *B. b. soudleyensis* (Plate 4, Figs 15, 16).

Broeggerolithus broeggeri globiceps (Bancroft)

Plate 2, Figs 7, Pl. 5, Figs. 1-6, Text-Figs. 5.7, 6.1.

1929. *Cryptolithus globiceps* Bancroft, p. 88, pl. 2, figs. 1, 2.
1938. *Cryptolithus globiceps* Bancroft; Whittington, p. 53, pl. 6, fig. 1.
1938a. *Cryptolithus globiceps* Bancroft; Whittington, p. 450.
1940. *Broeggerolithus globiceps* (Bancroft); Whittington, p. 245.
1947. *Broeggerolithus globiceps* (Bancroft); Harper, p. 155, 172.
1958. *Broeggerolithus globiceps* (Bancroft); Dean, p. 206, pl. 26, fig. 9.
1958. *Broeggerolithus soudleyensis* (Bancroft); Dean, p. 207, 222.
1960. *Broeggerolithus soudleyensis* (Bancroft); Dean, p. 115-117, pl. 17,
fig. 2-4.
1960. *Broeggerolithus* sp. (? nov); Dean, pp. 119-120, pl. 17, fig. 12.
1963. *Broeggerolithus globiceps* (Bancroft); Dean, pp. 11-15.

1975. *Broeggerolithus globiceps* (Bancroft); Hughes *et al.*, p. 580.
1975. *Broeggerolithus sp.* (?nov) (Dean); Hughes *et al.*, p. 580.
1979. *Broeggerolithus nicholsoni globiceps* (Bancroft); Rushton *in* Burgess and Holliday, p. 12.
1981. *Broeggerolithus nicholsoni cf. globiceps* (Bancroft); Rushton *in* Arthurton and Wadge, p. 19.
1988. *Broeggerolithus globiceps* (Bancroft); Morris, p. 38.

Diagnosis. Glabella distinctly tumid. Arcs I_n , I_1 , E_1 complete, arc E_2 complete or absent mesially. Pits become generally larger posteriorly. Prominent E_1 arc radial ridges. Recorded pit count ranges and means for $I_n = 19$; $I_1 = 18-26$ (22); $E_1 = 19-27$ (23); $E_2 = 18-22$ (20); E_2 termination = n-3.

Lectotype. An incomplete upper lamella cephalon showing a complete left hand fringe. Selected by Dean (1960, p.118) BM. In42076. from the Horderley Sandstone Formation (Longvillian) of Rookery Wood, Horderley, Shropshire.

Distribution. Most common in the Horderley Sandstone Formation associated with *Dalmanella lepta* and *D. indica* up into the Alternata Limestone (middle Longvillian - lower Woolstonian). It is also found in the Llanfyllin District of the Berwyn Hills and the Pwllheli District, Wales in beds of early Woolstonian age.

Description. Essentially the same morphology as *B. b. broeggeri* but the glabella is much more swollen. Mesially the pit arrangement varies slightly between specimens, pits in the E_2 arc may be absent anteriorly (Plate 5, Fig. 1) or sulcate with E_1 similar to *nicholsoni* (Plate 5, Fig. 2).

Discussion. Morphologically and statistically there are a great number of similarities between *B. b. globiceps* and *B. b. broeggeri*, $I_1 = 18-26$ (22) cf. 20-23 (21) and $E_2 = 18-22$ (20) cf. 18-22 (20), compare Plate 5, Figs. 1,2 with Plate 4, Figs. 23, 24 (see also Figs. 5.7 and 5.8). Generally *B. b. broeggeri* has a much more restricted range for the pit counts than *B. b. globiceps*. The size and shape of the

glabella in *B. b. globiceps* is distinct enough to be able to identify this subspecies from the stratigraphically older *B. b. broeggeri* (Plate 5, Fig. 6). Similarly, *B. b. globiceps* contains more E₂ pits and a more swollen glabella than *B. b. soudleyensis*. In the past *B. b. globiceps* has been synonymised with contemporaneous *B. nicholsoni* (Burgess and Holliday, 1979; Morris, 1988), but this view is not supported here because of the significant differences in morphology and fringe pit statistics (see below). The younger *B. b. globiceps* shows a larger, more swollen glabella and slightly higher pit counts e.g. E1 19-27 (23) cf. 19-23 (21) and E2 11-18 (15) cf. 18-22 (20).

Abnormalities. The specimen in Plate 5, Figs. 3 and 4 shows a swollen pit and Pl. 5, Fig. 7 shows early termination of E₂ arc and non-alignment of E₂ pits anteriorly.

Broeggerolithus nicholsoni (Reed)

Plate 2, Fig. 9, Pl. 5, Figs. 7-11, Text-Figs. 5.8, 6.1.

- 1910. *Trinucleus nicholsoni* Reed, p. 212, pl. 16, figs. 1-9.
- 1929. *Cryptolithus longiceps* Bancroft; p. 89, pl. 2, figs. 3, 4.
- 1929. *Cryptolithus gibbifrons* Bancroft; p. 75, table.
- 1930. *Cryptolithus* s.p. Stormer; p. 44, pl. 6, fig. 14.
- 1938. *Cryptolithus gibbifrons* (McCoy); Whittington, p. 52.
- 1938. *Cryptolithus* cf. *gibbifrons* (McCoy); Stubblefield, p. 52.
- 1940. *Cryptolithus discors* (Angelin); Thorslund, p. 154, pl. 12, figs. 1-3.
- 1940. *Broeggerolithus longiceps* (Bancroft); Whittington, p. 245.
- 1945. *Broeggerolithus longiceps* (Bancroft); Bancroft, p. 249.
- 1958. *Broeggerolithus longiceps* (Bancroft); Dean, p. 207, pl. 26, fig. 10.

1960. *Broeggerolithus simplex* Dean; Dean, p. 120, pl. 17, fig. 14.
1962. *Broeggerolithus nicholsoni* (Reed); Dean, p. 79, pl. 6, figs. 7, 11, 14, pl. 7, figs 1-12.
1962. *Broeggerolithus melmerbiensis* Dean; p. 81, pl. 6, figs. 10, 13.
1963. *Broeggerolithus longiceps* (Bancroft); Dean, p. 12, 15.
1963. *Broeggerolithus nicholsoni* (Reed); Dean, p. 11, 15.
- 1963a. *Broeggerolithus nicholsoni* (Reed); Dean, p. 61, 63, pl. 5, figs 1,2,5,8,9,11.
1966. *Broeggerolithus nicholsoni* (Reed); Whittington, p. 86, pl. 26, figs. 16, 17, 19-22; pl. 27, figs. 12-16, 18, 19; pl. 28, figs 2-5.
1968. *Broeggerolithus nicholsoni* (Reed); Greig *et al.*, p. 112.
1968. *Broeggerolithus longiceps* (Bancroft); Greig *et al.*, p. 114.
1975. *Broeggerolithus nicholsoni* (Reed); Hughes *et al.*, p. 580.
1975. *Broeggerolithus* sp. (Angelin); Hughes *et al.*, p. 580.
1975. *Broeggerolithus longiceps* (Bancroft); Hughes *et al.*, p. 580.
1977. *Broeggerolithus* cf. *nicholsoni* (Reed); Brenchley *et al.*, p. 71, pl. 1, figs. 7-9.
1977. *Tretaspis* cf. *ceryx* Lamont; Brenchley *et al.*, p. 70.
1979. *Broeggerolithus nicholsoni longiceps* (Bancroft); Rushton in Burgess and Holliday, p. 12.
1981. *Broeggerolithus nicholsoni* (Reed); Rushton in Arthurton and Wadge, p. 19.
1981. *Broeggerolithus nicholsoni* cf. *nicholsoni* (Reed); Rushton in Arthurton and Wadge, p. 19.
1981. *Broeggerolithus nicholsoni* cf. *longiceps* (Bancroft); Rushton in Arthurton and Wadge, p. 19.
1983. *Broeggerolithus* aff. *discors* (Angelin); Owen, p. 52, fig. 2 A-F.
1988. *Broeggerolithus nicholsoni* (Reed); Morris, p. 38.
1988. *Broeggerolithus longiceps* (Bancroft); Morris, p. 38.

1994. *Broeggerolithus nicholsoni* (Reed); Parkes and Palmer, p. 75, fig. 5.

Diagnosis. Arcs I_n to E_2 complete. Pits in arcs I_1 and E_1 become larger posteriorly, this leads to loss of radial alignment of pits posteriorly. Radial ridges absent. The recorded pit count ranges and means for $I_n = 19-26$ (22); $I_1 = 19-26$ (23); $E_1 = 19-27$ (23); $E_2 = 15-24$ (21); E_2 termination = n to $n-5$ ($n-3$); F pits = 14-31 (21).

Lectotype. An incomplete cranidium showing a complete right-hand side fringe. Selected by Dean (1962, p. 80) SM A29613, from the Lower Melmerby Beds (Longvillian) of the Alston Road cutting, Melmerby, Cumbria.

Distribution. Occurs in material assigned to the Longvillian and Woolstonian of Shropshire, Shelve Inlier, Wales, Northern England, Ireland, Scandinavia and Belgium.

Description. Cephalic outline is more rounded than the *B. broeggeri* species. The glabella is long, narrow and clavate. The fringe morphology is simple with the majority of specimens showing no radial ridges, although some specimens show anterior sulcate pits (Plate 5, Fig 7). Radial alignment of pits in all arcs is good apart from the posterior region of the fringe where the increase in pit size posteriorly in arcs I_n to E_1 leads to the loss of radial alignment.

Discussion. This species is readily identifiable by its simple fringe morphology compared to previous species. A great deal of synonymy has occurred to this species in the past; *B. simplex* Dean (Plate 5, Fig. 8) and *B. melmerbiensis* Dean, both species erected on one specimen and *B. longiceps* (Bancroft) (Plate 5, Fig. 9) are all synonymies supported here on statistical and morphological grounds. The three species generally show arc pit ranges which are contained in the ranges of the respective *B. nicholsoni* arcs, for example, E_1 pit range (mean) of *B. nicholsoni* = 20-27 (24), *B. simplex* = 22, *B. longiceps* = 19-23 (22) and *B. melmerbiensis* 25.5. All show the more rounded cephalic outline and lack of radial ridges characteristic of *B. nicholsoni*. Although some specimens of *B. longiceps* have a longer glabella and

B. melmerbiensis shows closely packed E₂ pits, these features are not considered distinct enough for the retention of those species (see Section 5.5, Fig. 5.7(g), Pl. 5, Figs. 9,). There is a second smaller specimen very similar to *B. melmerbiensis* which also shows closely packed E₂ pits from the same area, the significance of these is uncertain but a similar feature is seen within the Swedish *B. aff. discors* of Owen (1983) and a single specimen within the older *B. b. broeggeri* population. One specimen of *nicholsoni* from the Cross Fell Inlier shows small E₂ pits and numerous E₃ pits, these features are also seen in *B. discors* to a greater extent. The synonymy of *B. globiceps* is rejected as it has a more angular cephalic outline, prominent radial ridges and the occasional absence of E₂ arc pits mesially compared with *B. nicholsoni* (Plate 5, Figs. 1-6 cf. 7-10).

Abnormalities. Fringe repair and taphonomic abnormalities have been described in the past (Whittington, 1966; Owen, 1983). Non-radial alignment of a single pit is seen in the specimen in Plate 5, Fig. 11.

Broeggerolithus discors (Angelin)

Plate 2, Fig. 12.

1854. *Trinucleus discors* Angelin, p. 84, pl. 40, figs. 28a, 28b.

1857. *Trinucleus discors* Angelin; Kjerulf, p. 94.

1930. *Cryptolithus discors* [sic] Angelin; Stormer, p. 40-43, pl. 6, figs. 1-12.

1953. *Cryptolithus discors* Angelin; Stormer, p. 65.

1975. *Broeggerolithus discors* (Angelin); Hughes *et al.*, p. 580.

1978. *Broeggerolithus discors* (Angelin); Owen, p. 8.

1979. *Broeggerolithus discors* (Angelin); Owen, p. 246.

1979. *Broeggerolithus discors* (Angelin); Bruton and Owen, p. 219.

1982. *Broeggerolithus discors* (Angelin); Owen and Harper, p. 100.

1983. *Broeggerolithus discors* (Angelin); Owen, pp. 49-51, fig. 1, A-I.
1984. *Broeggerolithus discors* (Angelin); Owen in Harper and Owen, p. 33, pl. 5, figs. 22,23.
1985. *Broeggerolithus discors* (Angelin); Owen in Harper *et al.*, p. 298, figs. 2,4.

Diagnosis. All four arcs complete. E₂ arc pits small and closely packed with secondary loss of radial alignment laterally. The recorded pit count ranges for I_n = 23-28, I₁ = 23-27, E₁ = 26-29, E₂ = 30-40 and E₂ termination = n-1 to n-3. F pits = 29-33. (Data from Owen, 1983).

Neotype. Complete cranium. Selected by Stormer (1930); RM Ar2298, from the Nakkholmen Formation of Nakkholmen, Oslo.

Distribution. Material from the type unit Koksabukten at Fornebu, Oslo also present in other Marshbrookian-Actonian age material at Baerum, Hadeland and Ringerike (Owen, 1983).

Description. For a full description see Owen, 1983. Cephalic outline is more rounded than that of *B. broeggeri*. The fringe morphology is relatively simple with the concentric band between arcs I_n and I₁ being the only raised feature on the fringe. Radial alignment of arcs I_n to E₁ is generally good, though becomes irregular posteriorly in many specimens because of the increase in pit sizes in these arcs. The E₂ arc is composed of small closely packed pits which lose radial alignment with the inner arcs laterally. The close packing of E₂ arc pits leads to the appearance in some specimens of E₃ pits usually in sulcae with E₂ pits.

Discussion. This species is rather problematical as it contains a mixture of characters indicating the similarity both to *B. nicholsoni* and species of *Salterolithus*. Thus the closely packed E₂ pits, out of radial alignment with the inner arcs generally from the lateral area of the fringe towards the genal angle and the presence of an E₃ arc in most specimens are features of *Salterolithus*. The presence of high counts for the F pits is not seen in *Salterolithus* and generally not present in *B. nicholsoni*.

However, within the Cross Fell Inlier there are rare specimens of *B. nicholsoni* which show features very similar to *B. discors*, i.e. closely packed irregular E₂ pits and high F pit counts and one specimens showing a few E₃ pits (Plate 5, Fig 12). This close similarity between the rare *B. nicholsoni* forms and the Swedish aff. *discors* material placed in *Broeggerolithus* by Owen 1983, now synonymised with *nicholsoni* (see above), may show that *B. discors* is closely related to *B. nicholsoni* and is perhaps a descendent.

Broeggerolithus transiens (Bancroft)

Plate 2, Fig. 10, Pl. 5, Figs. 3-5, Text-Figs. 5.8, 6.1.

- 1929. *Cryptolithus transiens* Bancroft, p. 90, pl. 2, fig. 5.
- 1933. *Broeggeria transiens* (Bancroft); Bancroft, table 1.
- 1945. *Broeggerolithus transiens* (Bancroft); Bancroft, p. 196, 197.
- 1948. *Broeggerolithus transiens* (Bancroft); Bancroft in Lamont, p 417, 467.
- 1949. *Broeggerolithus transiens* (Bancroft); Bancroft, p. 298, pl. 9, fig. 8.
- 1958. *Broeggerolithus transiens* (Bancroft); Dean, p. 208, pl. 26, fig. 11.
- 1960. *Broeggerolithus transiens* (Bancroft); Dean, p. 123-126, pl. 18,
figs. 2, 3, 7, 8, 11-14.
- 1962. *Broeggerolithus* cf. *transiens* (Bancroft); Dean, pp. 82-83, 129, pl. 8,
fig. 1, 3, 4, 6, 8, 11.
- 1962. *Broeggerolithus* sp. Dean; pp. 83-84, pl. 8, fig. 2.
- 1963. *Broeggerolithus transiens* (Bancroft); Dean, pp. 5, 12, 15, pl. 1,
fig. 1-4.
- 1963. *Broeggerolithus* cf. *transiens* (Bancroft); Dean, pp. 12, 15.
- 1968. *Broeggerolithus transiens* (Bancroft); Greig *et al.*, p. 114.

1975. *Broeggerolithus transiens* (Bancroft); Hughes *et al.*, p. 580.

Diagnosis. Arcs I_n to E_2 complete. Pits appear in radial sulcae mesially on lower lamella. The recorded pit count ranges and means for I_n = 17-22 (19); I_1 = 17-22 (19.5); E_1 = 18-23 (21); E_2 = 16-22 (20); E_2 termination = $n-1$ to $n-4$ ($n-2$); F pits = 15-24 (19).

Holotype. An incomplete cranidium showing a complete left-hand side fringe. Selected by Dean (1960, p. 125); BM In42071, from the *Dalmanella unguis* Beds (Marshbrookian) of Marsh Wood, Marshbrook, Shropshire.

Distribution. In the South Shropshire upper Cheney Longville Flags (Marshbrookian) and lower Acton Scott Formation (Actonian) and the Dufton Shale Formation of the Cross Fell Inlier, Northern England (Marshbrookian).

Description. Cephalic outline rounded. Fringe morphology very simple. All four arcs are complete, with lower pit counts than earlier species. Pits contained in arcs I_n and I_1 increase in size posteriorly. Good radial alignment of pits over entire fringe. Pits within arcs E_1 and E_2 are sulcate anteriorly on lower lamella.

Discussion. This is the last of the *Broeggerolithus* lineage and shows a reversion to the simple form seen in the earliest specimens of this genus. The simple morphology and low pit counts enables easy differentiation from all the other species.

Abnormalities. The tearing of the outer fringe appears to be the cause of the fringe abnormality in specimen BMIn 50222 as seen in Plate 2, Fig. 10.

PLATE THREE

Salterolithus carataci (Murchison)

Upper Harnage Shale Formation, Upper Harnagian, *Salterolithus carataci* Biozone. Upper reaches of the stream section adjacent (south) of Wyrestche Quarry, Little Stretton, Shropshire, England.

- Fig. 1. Complete specimen, HM.A10420a, dorsal view, x2. Note non-radial alignment of E₂ pits.
- Fig. 4. Lower lamella, HM.A10421/b, ventral view, x4. Note irregular pit pattern of E₃ mesially.
- Fig. 5. Lower lamella, HM.A10423/2a, ventral view, x3. Specimen shows irregular pit pattern of E₃ arc producing some E₄ pits mesially.

Upper Trilobite Dingle Shale Formation, Upper Harnagian, *Salterolithus carataci* Biozone. Lower reaches of stream section, Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales.

- Fig. 2. Complete trilobite, HM.A22140a, dorsal view, x2. Specimen shows smaller non-aligned E₂ and E₃ pits.
- Fig. 3. Two cephalae, BM.In51894, dorsal view, x2. Note non-alignment of E arc pits and decrease in E pit size seen in both specimens.

Salterolithus harnagensis Bancroft, 1929

Morphotype A

["*Broeggerolithus harnagensis*"]

Lower Harnage Shale Formation, *Salterolithus harnagensis* & *Reuscholithus reuschi* biozone. Coundmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

- Fig. 6. Cranidium, HM.A10926b, dorsal view, x15. Shows strong reticulation and irregular E₂ pit positioning.

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Swampy ground at back of Caer Caradoc, Approx. 0.33 km west of Robin's Tump, The Cwms, Church Stretton, Shropshire, England.

Fig. 7. Cranidium and lower lamella, HM.A10443/2, dorsal view, x3. Impression of strong girder and long genal spines. Note partial alignment of E2 pits on left hand side and extra E2 pits on right hand side.

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Countmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 8. Cranidium, HM.A10855, dorsal view, x8. Shows extra E2 pits with thin walls dividing some pits. Alignment of all pits is seen mesially. All pits are of similar size.

Salterolithus harnagensis Bancroft

Morphotype B

["*Broeggerolithus harnagensis*" and "*Salterolithus praecursor*"]

Lower Harnagian Shale Formation, *R. reuschi* Zone. Swampy ground at back of Caer Caradoc, Approx. 0.33 km west of Robin's Tump, The Cwms, Church Stretton, Shropshire, England.

Fig. 9. Cranidium, HM.A10442, dorsal view, x2. All E2 pits showing non-radial alignment with inner arcs. All fringe pits are of similar size.

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Countmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 10. Fringe section of cephalon, BGS.RP264, dorsal view, x 4. Left hand fringe shows irregular outline and irregular pit distribution, possibly a result of an injury.

Salterolithus harnagensis Bancroft
Morphotype C
[“*Salterolithus praecursor*” and “*Salterolithus caractaci paucus*”]

Lower Trilobite Dingle Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Upper reaches of stream section, Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales.

Fig. 11. Complete trilobite, (N. Goodwin collection), dorsal view, x2. Note non-radially aligned E2 pits. Right hand side shows some E2 and E3 pits divided by thin wall.

Fig. 13. Fragment of fringe, latex cast, (N. Goodwin collection), dorsal view, x6. Note non-radial alignment of E2 pits and positioning of E3 pits. Irregular pit pattern mesially.

Trilobite Dingle Shale Formation, loose material in stream section, probably from *S. harnagensis* & *R. reuschi* biozone. Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales.

Fig. 12. Nearly complete individual, HM.A23145, dorsal view, x3. Note mesial and lateral position of E3 arc. L₁ to E₁ arc pits larger than outer arc pits. Close packing of E2 arc pits.

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Swampy ground at back of Caer Caradoc, Approx. 0.33 km west of Robin's Tump, The Cwms, Church Stretton, Shropshire, England.

Fig. 14. Cranidium, HM.A10438, dorsal view, x2. Specimen shows highly irregular pit pattern of E2 arc. E3 arc mesially. Some E2 and E3 arc pits divided by thin wall.

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Coundmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 15. Lower lamella, HM.A10875, ventral view, x2. Note highly irregular pit distribution in all E arcs.

PLATE THREE



PLATE FOUR

Salterolithus harnagensis Bancroft

Morphotype C

[“*Salterolithus praecursor*” and “*Salterolithus caractaci paucus*”]

Lower Harnage Shale Formation, *Salterolithus harnagensis* & *Reuscholithus reuschi* biozone. Countmoor Brook south bank, 65 metres below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 1. Probably meraspis cranidium, HM.A10915b, dorsal view, x15. Note strong reticulation, difference in pit sizes and non-radial alignment of E2 pits.

Lower Trilobite Dingle Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Upper reaches of stream section, Bron-y-Buckley Wood (Trilobite Dingle), Welshpool, Powys, Wales.

Fig. 2. Nearly complete individual, HM.A46414, dorsal view, x2. Note irregular fringe outline and pit distribution, possibly resulting from an injury.

Salterolithus harnagensis Bancroft

Morphotype D

[“*Salterolithus praecursor*”]

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Countmoor Brook south bank, 7.3m below weir, 3.5 km WSW of Cressage, Shropshire, England.

Fig. 3. Latex cast of cephalon, BM.In52031, dorsal view, x2. Note E3 arc extending posteriorly. E2 arc out of radial alignment.

Fig. 4. Latex cast of lower lamella, BM.In52036, ventral view, x2. Note prominent girder and pseudo-girder. Concentric ridges can be seen along the girder and broad pseudo-girder. Genal spine extends posteriorly.

Lower Harnagian, Smeathen Wood Formation, *S. harnagensis* & *R. reuschi* biozone. South west corner of Smeathen Wood, Onny River Valley, Cheney Longville, Church Stretton, Shropshire, England.

Fig. 5. Lower lamella, HM.A5469/5, dorsal view, x4. Note non-radial alignment of E2 pits. E3 arc pits closely packed. Indent mesially on inside edge of lamella aids a tight seal with the pygidium during enrollment.

Salterolithus harnagensis Bancroft

Morphotype E

[“*Smeathenia smeathenensis*”]

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Wyrestche Quarry, behind the stable, near the southern end of Ragleth Hill, Little Stretton, Shropshire, England.

Fig. 6. Cranidium, HM.A10433/1, antero-lateral view, x2. Note well spaced E4 arc pits extending posteriorly. E2 out of radial alignment with inner arc pits. Difference in pit sizes is seen between arcs I_n to E1 and E2 to E4.

Lower Harnagian, Smeathen Wood Formation, *S. harnagensis* & *R. reuschi* biozone. Southern area of Smeathen Wood, Onny River Valley, Cheney Longville, Church Stretton, Shropshire, England.

Fig. 7. Latex cast of cephalon, BM.In52006, dorsal view, x3. Note E4 arc pits extending to antero-lateral position. E2 out of radial alignment with inner arc pits. Difference in pit sizes is seen between arcs I_n to E1 and E2 to E4.

Morphotype F

[“*Smeathenia smeathenensis*”]

Lower Harnage Shale Formation, *S. harnagensis* & *R. reuschi* biozone. Woolston House, Woolston, Shropshire, England.

Fig. 8. Cranidium, BM.In50767, dorsal view, x 6. Note strong reticulation. Well spaced E4 arc pits extending posteriorly. E2 out of radial alignment with inner arc pits. Difference in pit sizes is seen between arcs I_n to E1 and E2 to E4.

Broeggerolithus broeggeri broeggeri (Bancroft)

[“*Broeggerolithus broeggeri*” and “*Broeggerolithus constrictus*”]

Lower Soudleyan, *B. b. broeggeri* Biozone, upper Chatwall Flags, band of decalcified sandy limestone from below the Chatwall Sandstone. Small, partly overgrown trackside exposure, The Pools, Chelmick Valley, Hope Bowdler, Church Stretton, Shropshire, England.

Fig. 9. Cranidium, HM.A18626/2, dorsal view, x2. Note strong radial alignment of all arcs, flexing outwards. Narrow concentric bands. Radial ridges developed.

Fig. 10. Cranidium, HM.A18618/1, dorsal view, x2. Note strong radial alignment of all arcs, flexing outwards. Specimen shows the most common mesial pattern of pits one E₁ pit between the two mesial radial rows..

Lower Soudleyan, *B. b. broeggeri* Biozone. North east corner of Smeathen Wood, Onny River Valley, Cheney Longville, Church Stretton, Shropshire, England.

Fig. 11. Latex cast of near complete trilobite, BM.In48937, dorsal view, x2.

Note strong radial alignment of all pits, increased size of E₁ pits posteriorly, E₁ arc appears raised higher than other arcs due to prominent radial ridges. Note distinct curve in fringe outline after E₂ arc terminates posteriorly.

Basal Soudleyan. Millpond, SW of Caunant, Welshpool, Powys, Wales.

Fig. 12. Latex cast of part of cranidium, BM.In42101, dorsal view, x3. Note strong radial rows E₁ pits larger posteriorly. Prominent radial ridges. Note distinct curve in fringe outline after E₂ arc terminates posteriorly.

Lower Soudleyan, *B. b. broeggeri* Biozone. North east corner of Smeathen Wood, Onny River Valley, Cheney Longville, Church Stretton, Shropshire, England.

Fig. 13. Cephalon, BM.In50507, oblique, antero-lateral view, x3. Note very short E₂ arc. E₂ pits in radial alignment with inner arc pits. Radial ridges are visible.

Rare form within *broeggeri* population.

Fig. 14. Cephalon, BM.In50507, oblique, antero-lateral view, x3. Note very short E₂ arc. E₂ pits in radial alignment with inner arc pits. Radial ridges are visible. Rare form within *broeggeri* population.

Broeggerolithus broeggeri ulrichi (Bancroft)
[“*Broeggerolithus ulrichi*”]

Upper Harnagian, *Broeggerolithus b. ulrichi* Biozone, stream section in Middle House Dingle, Powys, Wales.

Fig. 15. Partially complete individual, BM.In51865, dorsal view, x6. Note strong radial alignment of all pits. Raised E₁ arc, achieved by radial ridges.

Fig. 16. Latex cast of part of a cephalon, BM.In51897, dorsal view, x2. Note strong radial rows of all pits except some E₂ pits mesially. E₁ arc appears raised higher than other arcs because of prominent radial ridges.

PLATE FOUR

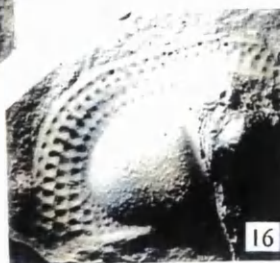
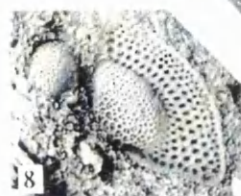


PLATE FIVE

Broeggerolithus broeggeri globiceps (Bancroft)
[“*Broeggerolithus globiceps*”]

Lower Longvillian. South east Capel Peniel, Llanbedrog, Caernarvonshire, Wales.

Fig. 1. Latex cast of lower lamella, BM.In54098, ventral view, x3. Note E2 pits absent laterally. Prominent girder.

Lower Woolstonian, Alternata Limestone, Member of the Cheney Longville Flags, *K. bipartita* Biozone. Soudley Quarry, The Pools, Chelmick Valley, Hope Bowdler, Church Stretton, Shropshire, England.

Fig. 2. Incomplete cephalon, HM.A11984a, oblique antero-lateral view, x3.
Specimen shows strong broad radial ridges on upper lamella.

Lower Longvillian, Middle Horderley Sandstone Formation, *D. lepta & indica* biozone. Quarry at top of west end of Rookery Wood, Horderley, Shropshire, England.

Fig. 3. Complete cranidium, BM.In49313, dorsal view, x2. Note strong radial alignment of all pits. Prominent radial ridges.

Fig. 4. Complete cranidium, BM.In49313, antero-lateral view, x2. Note strong radial alignment of all pits. Alignment of pits persists to genal angle.
Prominent radial ridges.

Fig. 5. Incomplete cranidium, BM.In49315, dorsal view, x3. Note prominent glabella, strong radial alignment of all pits.

Lower Woolstonian, Alternata Limestone Member of the Cheney Longville Flags, *Kjaerina bipartita* Biozone. One kilometre west of Cheney Longville, Shropshire, England.

Fig. 6. Incomplete cranidium, HM.A5468, dorsal view, x4. Rare specimen showing irregular pit positioning and early termination of E2 arc. Reticulation faintly visible.

Broeggerolithus nicholsoni (Reed)

Longvillian, Lower Melmerby Beds, Dufton Shale Formation, Cross Fell Inlier. Alston Road cutting. near Melmerby, Cumbria, England.

Fig. 7. Cranidium, SM.A29613, antero-lateral view, x3, lectotype. Note radial sulcae mesially. Some loss of radial alignment of pits posteriorly.

Lower Longvillian, Horderley Sandstone Formation, *D. lepta* and *indica* Biozone. Just east of the south-western corner of Rookery Wood, Horderley, Shropshire, England.

Fig. 8. Incomplete cranidium, BM.In50614, dorsal view, x3, *B. simplex* lectotype. Note strong radial alignment of all pits and radial sulcae mesially.

Lower Woolstonian, Alternata Limestone, Member of the Cheney Longville Flags, *Kjaerina bipartita* Biozone. From stream on west side of road from Horderley to Marshbrook, about one kilometre north-north-east of Whittingslow, Shropshire, England.

Fig. 9. Incomplete cephalon, BM.In42073, dorsal view, x2, [lectotype of *B. longiceps* (Bancroft)]. Note strong radial alignment of all pits.

Longvillian, Corona Beds, Cross Fell Inlier. East of Hilton, Westmorland, Cumbria, England.

Fig. 10. Latex cast, BM.It9017, dorsal view, x2. Note strong radial alignment of pits, lost posteriorly.

Woolstonian, Dufton Shale Formation, Cross Fell Inlier. In stream, Harthwaite Sike, near Bow Hill, near Brough-under-Stainmore, Cumbria, England.

Fig. 11. Incomplete cranidium, BGS. PJ3728, antero-lateral view, x3. Note strong radial alignment of pits. Break down of alignment towards the genal angle. Some pit disruption seen laterally.

Fig. 12. Latex cast of incomplete cephalon, BGS. PJ3702, dorsal view, x3. Note strong radial alignment of pits. Seven small pits visible at postero-lateral margin of fringe.

Broeggerolithus transiens (Bancroft)

Actonian, Acton Scott Formation. One metre above floor of quarry, Acton Scott Quarry, Old Quarry, 460 metres west-north-west of St. Margret's Church, Acton Scott, Shropshire, England.

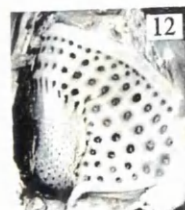
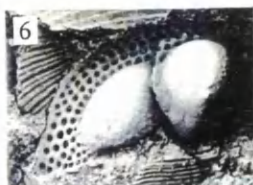
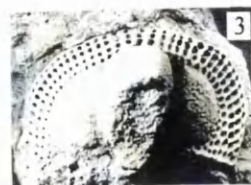
Fig. 13. Incomplete cranium, HM.A23082a, dorsal view, x2. Note strong radial alignment of all pits, which persists posteriorly.

Fig. 15. Incomplete cephalon, HM.A23081, dorsal view, x3. Note distinct girder and genal spine and strong radial alignment of pits which persists posteriorly.

Marshbrookian, Upper Cheney Longville Flags, *Dalmanella unguis* Biozone. Top section at north end of quarry one and a half kilometres south of Marshbrook Station, Marshbrook, Shropshire, England.

Fig. 14. Latex cast of near complete cranium, BM.IN52051, dorsal view, x2. Note strong radial alignment of pits which persists posteriorly.

PLATE FIVE



8 Possible Origins Of The Anglo-Welsh Cryptolithinae

At the beginning of the Harnagian the trilobite populations in the Welsh Borderland were dominated by the species *Reuscholithus reuschi* a member of the *Marrolithinae* and by the appearance of the *Salterolithus*, which over a relatively short period of time displaced *R. reuschi* and became the dominant trilobite. This suggests that *Salterolithus* was a migrating opportunist for which there is no ancestral evidence in Britain. Similarly, *Onnia* (a marrolithine) found in the Welsh Borderland was referred to by Owen and Ingham (1988) as a peri-Gondwanan immigrant. Until gaps in its ancestral record are filled the origins of *Salterolithus* can only be speculated upon.

The subfamily Cryptolithinae contains the Anglo-Welsh genera studied herein with their fixed number of I arcs and variable E arc numbers and two North American and one Czech Republic genera; *Cryptolithus*, *Cryptolithoides* and *Marekolithus* whose I arcs are variable whilst their E arc is fixed at one. In no area in which cryptolithines are found are there any credible ancestors.

The Marrolithinae of Hughes (1971) have E_1 , I arcs and flange pits in ordered distribution but are characterised by the I_n arc being “cut-off” laterally by the adjacent I arc. They are found in deposits from the Llanvirn to late Caradoc, essentially in a Gondwanan context. The genus *Reuscholithus* was the dominant early Harnagian marrolithine in southern Britain when the migrant *Salterolithus* became established within the Anglo-Welsh basin. In the Reedolithinae of Hughes *et al.* (1975) there are no F pits other than the posterior fossula and these trinucleids have eye tubercles and ridges. They are found in the Caradoc from Scotland, Ireland, Norway, Quebec, Argentina and possibly China. In the subfamily Trinucleinae of Hawle & Corda (1847) there is a well furrowed glabella and well ordered E and I pits commonly sulcate on the upper lamella and no F pits, other than the posterior fossula. They are present in the Arenig to Ashgill deposits and are widely distributed globally, although some stocks appear to have a more restricted geographical distribution. Finally, the Hanchungolithinae of Lu (1963), show a simple fringe morphology with marginal or

submarginal girder, irregular distribution of I pits and no F or E pits. They are found in the lower Arenig of Wales (Beckly, 1985, Fortey and Owens, 1987), SE Ireland (Brenchley and Skevington, 1967), southern France (Dean, 1966), the Arenig of central China (Zhou and Hughes, 1989), possibly upper Llanvirn of Argentina and the middle Ordovician of Iran (Hughes *et al.*, 1975 and Zhou, 1989).

The genus *Yinpanolithus* Lu (*in* Lu and Chang, 1974) was included in the Trinucleinae by Zhou and Hughes (1989) as it contains no F pits other than the posterior fossula, and there are no indications of I_n cut off laterally by adjacent I arc. *Yinpanolithus* is found in late middle and late Arenig strata from south-west, central and south-east China. There is, however, a similar cephalic and fringe morphology to cryptolithines generally with well ordered I and E arcs. The type-species *Yinpanolithus yinpanensis* Lu (*in* Lu and Chang, 1974) shows remarkable similarities to *Broeggerolithus broeggeri*, for example, I_n and I_1 arcs contain large, well ordered and radially aligned pits, sulcate anteriorly. A well developed girder, marginal frontally but not laterally, suggests the development of at least one E arc posteriorly (see Lu and Chang, 1974, pl. 15, fig. 9; Zhou et al., 1977, pl. 74, figs. 5 and 6 and Lee, 1978, pl. 109, fig. 5.). The type-locality of *Y. yinpanensis* is the Yinpan Formation, late middle to late Arenig from Yangjiaba, Chengkou County (loc. 17) north-eastern Sichuan. It has also been found in late middle Arenig of the Dawan Formation, Xiaoguanshan, Xianyang County (loc. 23), Hubei Province. *Y. guizhouensis* Yin (*in* Yin and Lee, 1978) from the upper part (late Arenig) of the Meitan Formation of Heishixi, Tongzi County (loc. 11), northern Guizhou and *Y. tenuilimbatus* Zhang (*in* Qui *et al.*, 1983) from the lower part (late Arenig) of the Xiaotan Formation, Shinianpan, Hexian County (loc. 25), Anhui Province are similar in all essential to the type species, only differing in minor morphological details. The species *wutangensis* is another which shows similar morphology to the cryptolithines. Originally described as "*Trimucleus*" *wutangensis* by Lu (*in* Wang et al., 1962) it has since been placed in *Yinpanolithus* by Zhou and Hughes (1989). The species occurs in the late Arenig of the Meitan Formation of Housuo, Wutang, near Guiyang City

(loc. 13), Guizhou. Specimens show a submarginal girder along the entire fringe evidently with no E arcs but with well ordered I_n and I_1 arcs laterally (see Lu, 1962, pl. 13, fig. 13 and Lu, 1965, pl. 124, figs. 7 and 8, note fig. 7 same as Lu, 1962 figure). These differences suggest that *wutangensis* represents a new genus, nevertheless closely allied to *Yinpanolithus*.

The revised lower age range for the Chinese Hanchungolithinae as Arenig and not Llanvirn as originally thought (Lu, 1963), would suggest that they coexisted with the early Trinucleinae and shared a common ancestry (see Fortey and Owens, 1987). The strong cryptolithine morphology of *Y. yinpanensis* and its allies in the Chinese Arenig is suggestive of a possible ancestral stock for the N.W. European and the N. American Cryptolithinae and these may also share a common ancestry, presumably in the Tremadoc, with undoubted trinucleines and hanchungolithines.

If this suggested ancestry is correct then the Cryptolithinae, with minor revision, could include *Yinpanolithus*, "*Y*". *wutangensis*, *Cryptolithus*, *Cryptolithoides*, *Marekolithus*, *Salterolithus* and *Broeggerolithus*.

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